

MYCOLOGIA

OFFICIAL ORGAN OF THE MYCOLOGICAL SOCIETY OF AMERICA

Vol. XLVII NOVEMBER-DECEMBER, 1955 No. 6

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[MYCOLOGIA for September-October (47: 619-778) was issued October 7, 1955]

PUBLISHED BIMONTHLY FOR
THE NEW YORK BOTANICAL GARDEN
AT PRINCE AND LEMON STS., LANCASTER, PA.

Entered as second-class matter April 30, 1935, at the post office at Lancaster, Pa., under the Act of August 24, 1912.

MYCOLOGIA

Published by

THE NEW YORK BOTANICAL GARDEN

IN COLLABORATION WITH THE

MYCOLOGICAL SOCIETY OF AMERICA

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XLVII

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No. 6

ARE FUNGI PLANTS?¹

G. W. MARTIN

"... scientific work is in its essence fluid and progressive, and from time to time it outdistances the principles which formerly it had assumed as basic. It is thus necessary to scrutinize them repeatedly and, if need be, to subject them to drastic revision." Agnes Arber, *The Mind and the Eye*. 1954.

Are fungi plants? It is probable that an overwhelming majority of botanists and a substantial number of those whose particular interest is with fungi would answer this with an unqualified affirmative. If we deduct from the latter group the plant pathologists, physiologists, and others who are primarily concerned with what fungi do rather than with what they are (although certainly the two aspects are inextricably combined), it is probable that the majority would still answer in the affirmative, but by no means overwhelmingly so, and with many qualifications. Nevertheless, in nearly all general works on botany and in many special treatises on fungi, it is explicitly stated or tacitly assumed that fungi *are* plants. Such terms as Mycothallophyta, Myxophyta, Mycophyta designate the included organisms as comprising plant groups; the feminine endings often used for such names as Phycomycetae, Ascomycetae, Basidiomycetae, to agree with the inferred Plantae; the reference to gametophytic and sporophytic generations in life cycles; these all emphasize the popular view.

I do not expect to answer the question I have posed. I propose only to examine some of the reasons why fungi have for so long been

¹ Sixth annual lecture of the Mycological Society of America, East Lansing, Michigan, September 8, 1955.

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accepted as members of the plant kingdom, to point out that over a period of many years objections have been made to this concept and to suggest that it may be desirable to consider these objections in the same spirit with which we should reexamine any opinions which, by reason of long familiarity, we take for granted.

When, over two centuries ago, Linnaeus published the aphorism: "Lapides crescunt; vegetabilia crescunt & vivunt; animalia crescunt, vivunt & sentiunt," he was not stating anything new but merely expressing a belief which went back to classical tradition—something which he, in all probability, would have regarded as axiomatic. His predecessors, represented by Micheli, and his contemporaries, such as Battarra, showed in many of their illustrations "roots" of fungi and quite evidently regarded them as homologous in structure as in function with the roots of the herbs with which they were associated. Obviously, to them, as to many at the present time, fungi were not mineral, they were certainly not animal, therefore they must be vegetable. Animal, vegetable, mineral exhausted the possibilities. It is necessary to stress this, since much of what has been written on the subject up to the present time suggests that the writers, in interpreting evidence which seems to bear on the matter, are often biased by deep-seated, and perhaps unrecognized, preconceptions.

To Linnaeus, as to his predecessors and contemporaries, fungi were known chiefly in the form of the large, fleshy, terrestrial agarics, boletes, puffballs, phalloids, morels and cup-fungi, and the obviously similar and predominantly poroid fungi growing on wood. To them, a mushroom on a forest floor, with its often evident rhizomorphs, seemed as distinctly a plant as many of its neighboring herbs,² and the extension of the concept to include polypores "rooted" in decaying wood was entirely natural. Such extension once made, it was equally natural, as more and more of the microfungi became known, to broaden the concept by imperceptible degrees to include them. This has culminated in such absurdities, by no means unusual even today, as reference to a *Penicillium* or *Botrytis* conidiophore, with its conidia, as a plant. And it is very common, in current literature, to find the individual fructification of an agaric or a polypore—perhaps one of several or of several hundred developing simultaneously on the same mycelium—referred to as a "plant." Admittedly, there is a certain superficial analogy to such an aggregation in the mass of units composing a moss colony, or a cluster

² An exception is Wiggers (1780), who expressed doubt whether fungi should be regarded as plants. None of his contemporaries, so far as I am aware, paid any attention to this heresy.

of ferns or shrubs, but a little reflection will show that the units of any such group are fundamentally quite different in nature and function from an aggregation of fungal fructifications. A better comparison would be with the apples on an apple tree or the grains in a head of wheat, which, as specialized structures concerned with reproduction, are very roughly comparable with the individual fungal fructifications. The mycelium, equally roughly, is similarly comparable with the tree or herb bearing the fruit, with the relatively unimportant difference that it happens to be out of sight. But neither the apple nor the grain is referred to as a plant. The application of the term to the individual mushroom or other fungal reproductive structure has far less warrant.

My own interest in this subject dates back to the time, many years ago, when I had opportunity to study the Dinoflagellates. Until that time, I had not seriously questioned the currently accepted opinion, advocated in most of the books with which I was then familiar, that the fungi had been derived from the algae by loss of chlorophyll. Here I was confronted with a group of organisms, obviously closely related on the basis of the criteria afforded by morphology and cytology, in which nutrition could be holozoic, holophytic, saprobic or parasitic, sometimes with holozoic and holophytic species assigned to the same genus. In other words, in what we have every reason to believe is a natural group of organisms, we find all available methods of acquiring nutrition, save only chemosynthesis. And I was immediately impressed by the statement of Kofoed and Swezy (1921) that there was no evidence that the saprobic forms were to be regarded as having been derived from those with chlorophyll.

Shortly thereafter I began the study of the Myxomycetes, again starting with the conviction, which I regarded as substantially proved, that these organisms were definitely animals and that their association with the fungi was based on inaccurate comprehension and long tradition, and nothing more. The considerations which impelled me to change this opinion I have already discussed at some length (Martin 1932, 1940) and it is necessary to say here only that I concluded that the Myxomycetes constitute a side line related to the lower fungi but by no means so primitive as sometimes considered, and that they have no connection with any of the so-called higher fungi. As indicated later, I should now be inclined to modify this conclusion, but not in such fashion as to exclude the Myxomycetes from the fungal series.

Even before the theory of Darwin was promulgated, resulting in wide acceptance of the concept of evolution, Alexander Braun (1847) declared unequivocally that the fungi were collateral groups of algae,

and Pringsheim (1858) argued that the possession of zoospores by the Saprolegniaceae was in itself enough to show that these were algae and that the type of sexual reproduction they possessed was additional and conclusive evidence of such relationship.

One immediate effect of the acceptance of evolution was to stimulate phylogenetic speculation, eventually resulting in two quite different views as to the nature and relationships of the fungi, one deriving them from algae, the other from animal-like Protista.

The earlier of the algal phylogenies carried on the tradition established by Braun and Pringsheim, that the fungi constitute an essentially heterogeneous assemblage, derived from various groups of algae. Somewhat later schemes approached more or less a monophyletic derivation, nearly always with exclusion of the Myxomycetes and associated organisms and often with exclusion of the Archimycetes, as variously defined. In all of these classifications it was taken for granted that all life must have been dependent upon food elaborated by photosynthetic organisms and that these must, therefore, have preceded heterotrophic forms. Since what were regarded as the morphologically simplest and presumably most primitive photosynthetic organisms were algae, the most attractive hypothesis to account for the fungi was that they had been derived from the algae by loss of chlorophyll. In the polyphyletic systems, the water molds are usually derived from such genera as *Oedogonium* or *Vaucheria*, the mucors from the *Spirogyra* group, and the Ascomycetes and the rusts, and through the rusts, or independently, the remaining Basidiomycetes, from the red algae.

Cohn (1872), following the lead already suggested by Braun and Pringsheim, and arguing that reproduction is basic and all other characters are secondary, arranged the fungi and algae into orders, many of which included representatives of both groups. In the Strasburger text, which first appeared in 1894, and which, with its numerous revisions, is probably by far the most influential botanical text which has ever been written, the algae and fungi are treated separately, but there is complete acceptance of the polyphyletic view (see 14th ed. by Fitting *et al.*, 1919) and while earlier combined groupings are not followed, it is clear that the various authors are agreed that sooner or later the fungi must be interpolated among the algal groups. This is done by Harper (1899), C. E. Bessey (1905) and Lotsy (1907). E. A. Bessey (1935, 1942, 1950) favors this view. The part of this theory particularly concerned with the derivation of the Ascomycetes and the rusts from the red algae has been discussed by many authors, notably by B. O. Dodge (1914), with special reference to the Ascomycetes, who

based his argument on what he believed to be the homology between the ascogonium and the carpogonium, by Orton (1927), and by Jackson (1944). The last-named, emphasizing the rusts, brings the argument up to date and concludes that it may tentatively be postulated that there were three lines of development leading from the red algae to the higher fungi, one to the Ascomycetes, one to the hymenomycetes and one to the rusts. There can be no question concerning the striking similarities between the groups under consideration which are brought out in these arguments. There are, however, marked differences which, in my opinion, are not adequately accounted for in these theories. Wholly aside from the radically different physiology of the algae and fungi, the differences in nuclear condition and in cellular organization and development are not satisfactorily explained and the attempt to homologize ascogenous hyphae and floridean gonimoblast filaments seems extraordinarily forced.

The most extreme and uncompromising assertion of the polyphyletic view is that of Clements and Shear (1931). They define a fungus as "a physiological adjustment to the environment" and add, "fungi are to be found in every major division of the plant kingdom; though rare among mosses and ferns, they are far from uncommon in the flowering plants." Leaving aside the dubious reference to mosses and ferns, the assignment of non-chlorophyllous angiosperms to the fungi on a physiological basis represents a startling extension of what is meant by fungi. It also fails to take into account the fact that the so-called saprophytic angiosperm genera, represented by *Monotropa* and *Corallorhiza*, secure their nutrients through the intermediation of mycorrhizal fungi, and might, indeed, with some reason be said to be parasitic on such fungi. Their nutrition is, therefore, quite different from that of the larger terrestrial fungi with which they are associated and with which they are frequently compared in this respect. It is also true that such algal genera as *Rhodochytrium* (Griggs, 1912) and the rather large number of parasitic Florideae which lack chlorophyll (Setchell, 1914, 1918, 1923) are still almost universally regarded as algae and not as fungi.³

In many of these theories, much is made of reduction and of what is called degeneration. Reduction is certainly an extremely useful concept and there is excellent evidence that it may legitimately be used as a hypothetical explanation of what may well have happened in many evolutionary sequences, including certain of

³ Clements and Shear, following Saccardo, do list *Rhodochytrium* as a genus of uncertain position, but ignore the red algae.

those in the fungi. But its very obvious pertinence in certain areas has encouraged its extension to a degree which seems to go far beyond its legitimate application and which can often be regarded only as wholly unsupported speculation. An example would be the supposed origin of the chytrids from water-molds with extensive mycelium. This theory is discussed at length by Atkinson (1909), who makes the point that there is no reason to suppose that the adoption of a parasitic mode of life would have the effect of favoring reduction of mycelium. In my opinion, Atkinson's arguments, so far as they apply to the chytrids at any rate, have never been convincingly refuted.

Degeneration, as used in this connection, may mean essentially the same thing as reduction, that is, morphological simplicity as compared with presumptive ancestral forms, even though such morphological simplicity may, as in the yeasts, be coupled with a high degree of physiological specialization. More often, degeneration means no more than supposed ancestral loss of chlorophyll, and resulting dependence on food secured directly or indirectly from green plants. If lack of chlorophyll, as compared with its possession, is a mark of degeneracy, it would appear that the human species, like all animal species, is degenerate. However valid, on other grounds, such a conclusion may be, the argument from lack of chlorophyll would not ordinarily be regarded as convincing.

The extreme polyphyletic views were not universally accepted. What are essentially monophyletic derivations of the great majority of the fungi from simple algae were developed by Winter (1879), de Bary (1881, 1884), Brefeld (1889), and Gäumann (1926). A. Fischer (1892) and Atkinson (1909) are sometimes cited as favoring this view, but Fischer quotes Dangeard's then recent work with approval and Atkinson specifically states that he would trace the lower fungi from either colorless or chlorophyll-bearing unicellular forms. De Bary excluded the Myxomycetes and similar forms from the Fungi, as did Brefeld, and Gäumann adds to these the holocarpic, endobiotic, naked Archimycetes, which he concludes represent an entirely distinct line from the myxomycete-flagellate complex. In his later book, Gäumann (1949) modifies his earlier conclusions, deriving the Oomycetes from the Siphonales and the rest of the fungi, including the Monoblepharidales and the Blastocladales, from the flagellates, suggesting, however, that the derivation is in all probability polyphyletic, and quite distinct from the flagellate series leading to the myxomycete groups.

Another effect of the evolutionary hypothesis was the conviction, first advocated by Huxley in 1868, that life must have developed by

imperceptible degrees from lifeless material. The early speculations on this subject are now mainly of historical interest, but they did succeed in impressing on many the artificiality of attempting to draw a sharp line between animals and plants at the morphologically simpler levels. Haeckel's concept of the Protista as embracing both plant-like and animal-like groups, advanced in the late 60's and summarized in his "Phylogenie" (1894), has had and continues to have substantial influence. It opened the way to consideration of the possibility that the fungi may have been derived from simple animal-like forms. The earliest suggestion to this effect seems to have been made by Gobi in 1884, presumably under the influence of Haeckel's earlier work. Gobi's paper, in Russian, is known to me only through the abstract by Borodin (1885), but he seems to have linked the forms grouped by Gäumann in the Archimycetes with amoeboid predecessors, and to have derived the chytrids and the oomycetes from these Archimycetes. Even earlier, Cornu (1872) had pointed out errors of fact in Pringsheim's discussion and consequent objections to Pringsheim's theories. Dangeard (1886) suggested a monophyletic system for the fungi and proposed that the method of nutrition be made the criterion to distinguish plants from animals. If food is taken into the interior and there digested, the organism is an animal; if the food is digested at the surface and the products absorbed, leaving the residues outside, it is a plant. This criterion, of course, makes the fungi plants, but ignores the existence of Protozoa and worms with similar nutrition. In later papers, Dangeard (1902, 1903) gives his considered opinion that the plant series have been derived by several lines of descent from the animal series, represented by the simpler Protozoa; the fungi represent one such series. Scherffel, slightly earlier (1901), argued for the derivation of the Myxomycetes and Archimycetes from amoeboid Protozoa and of the remaining Phycomycetes from the Archimycetes. In a later paper (1925) he provided many examples favoring this hypothesis based on detailed study of numerous species. The lower Phycomycetes, although derived from animal-like forms, have attained what he regards as plant-like nutrition in the same sense in which that is understood by Dangeard, that is, by absorption through membranes rather than by ingestion. Cavers (1915) argued for the derivation of the lower fungi from Protozoa. This view was further developed by Cook (1928) and by myself (Martin 1932). Smith (1938) recognized seven independent algal series hypothetically derived from an unspecified but presumably chlorophyll-bearing primitive stock. The Eumyceteae, i.e. the fungi, exclusive of the Myxomycetes and associated groups, he would regard as

a monophyletic series derived from Protozoa. In the second edition (1955) he makes the separation between the myxomycete groups and the remaining fungi, now called the Eumycophyta, more explicit in his diagram of suggested interrelationships. Sparrow (1943) expresses substantial agreement with Scherffel's views. Langeron (1945) argues strongly against the derivation of the fungi from algae. This is repeated by Langeron and Vanbreuseghem (1952) and it is proposed to extend the concept of non-cellular organisms, originating with Dobell (1911), to all of the fungi. Heim (1952) argues strongly for a monophyletic derivation of the fungi from Protozoa and points out many of the weaknesses in the arguments advanced in favor of the algal theories. Savile (1955) accepts the monophyletic view and appears to favor derivation from Protozoa, although he is chiefly concerned with the place of the rusts in the series.

The most recent extensive treatment of the fungi is that of Moreau (1954). Admittedly a follower of Dangeard, he modifies the latter's monophyletic system, suggesting that primitive protozoans have given rise to four independent groups of chytrids which he calls the Proso-mastigochytridiales, the Opisthomastigochytridiales, the Dimastigochytridiales and the Amastigochytridiales. The Proso-mastigochytridiales, having zoospores with one anterior flagellum, have gone no further. The Opisthomastigochytridiales, with one posterior flagellum, have given rise to the Monoblepharidiales and the Blastocladiiales. The Dimastigochytridiales, with two flagella, have given rise to the remaining Oomycetes. The Amastigochytridiales, without flagella, have given rise to the Zygomycetes, the Periascomycetes and the Dangeardiomycetes, the latter group including the great bulk of the Ascomycetes and all of the Basidiomycetes. The Myxomycetes and associated groups are excluded.

I have cited Moreau's arrangement rather fully, because I believe it comes nearer to the system which I should now favor than any other which has been proposed up to the present time. I should include the Myxomycetes in the strict sense, that is, the Exosporeae and the Myxogastres, and also the Plasmodiophorales, in the biflagellate series, but would, for the present, regard such groups as the Acrasieae and the Labyrinthuleae as representing independent lines of development. The recent work of Spiltoir and Olive (1955) and of Spiltoir (1955), which was not, of course, known to Moreau, necessitates reexamination of the relative rank given to the Periascomycetes. This system, as already noted, approaches the type of arrangement Smith has suggested for the algae.

We have become so accustomed to a tree-like phylogenetic system,

showing a single trunk with two great branches near the base, one leading to the animals, the other to the plants, that it may be difficult for a time to realize that what we have taken for a tree becomes, on nearer approach, a thicket, dominated by two or three larger trees and with associated shrubs, herbs and smaller components, all independently rooted (see Rogers, 1948).

I have referred to the often-repeated statement that green plants must have preceded animals and fungi, otherwise, these would have been unable to secure nutrients. Vuillemin (1907) pointed out that we cannot assume that at the remote epoch when life appeared conditions on the earth's surface were the same as at present and suggested that there may have been other autotrophs, citing the nitrogen-fixing bacteria as examples of organisms having a type of food-making quite distinct from that of green plants. Cavers (1913) cites Vuillemin's work with approval and, in a later paper (1915), suggests consideration of the photosynthetic and chemosynthetic bacteria in this connection, as organisms which have the capacity to synthesize organic compounds by methods different from those available to green plants. Bernal (1951) points out that such of these as contain complex enzymatic systems cannot be representative of the most primitive organisms.

Urey (1952) presents geophysical arguments supporting the suggestion, earlier advanced by Oparin (1938) and developed by Bernal (1951), that life may have begun under atmospheric conditions wholly unlike those that prevail at the present time, notably in lack of oxygen, and under circumstances favorable to the elaboration of organic compounds by chemical action. Miller (1953, 1955) produced experimental evidence supporting Urey's arguments when he synthesized several amino acids by circulating a mixture of heated methane, ammonium, water vapor, and molecular hydrogen past an electrical field in an oxygenless system. Gulick (1955) discusses the problem with special reference to the possible role of phosphorus in the linkage of polypeptide chains, on the hypothesis that life originated under conditions in which phosphorus was only partially oxidized. This work makes it clear that the argument that green plants must have preceded non-chlorophyll-bearing organisms because only green plants could have provided suitable nutrients has no basis in what we can infer as to the conditions under which life originated.

Whether, under the conditions postulated in these theories, life originated at one particular time and place or independently at various times and places, we can at present only guess. If it was the former, then all inheritance must, in the final analysis, be monophyletic. But

such a conclusion is highly theoretical and cannot, in the light of our present information, be presented as fact. It has been argued that the cytological features and the enzymatic systems of the overwhelming majority of known plants and animals strongly suggest a common origin. This is not completely convincing. What is postulated is a series of gradual chemical changes, all tending in the same direction, taking place on a planet with a presumably more uniform surface than at present, but scarcely completely uniform. If there were local variations in conditions, why is it necessary to suppose that they could not have been reflected in slight, but significant differences in the compounds which were being formed? Such differences would provide the requisite basis for the further differentiation in later times which we know has occurred. The picture of a gradual, orderly and widespread development from non-living to living is surely more in accord with what we know of natural processes than is that of a sudden, unique and isolated phenomenon.

The further point, that once living matter had succeeded in occupying the available habitats on the earth's surface, all available compounds suitable for origination of life would promptly be appropriated by them, is highly plausible. But if there were many essentially simultaneous local developments we are not justified in inferring that the spread of one of them was so rapid that all others were suppressed. The conception of a single living unit—"the protoplasmal primordial atomic globule," so proudly cited by Pooh-Bah as his ultimate ancestor—perhaps belongs more properly in the realm of comic opera than in serious scientific discussion. So far as the fungi are concerned, the possibility of independent origin appears to be restricted to the Myxomycetes, the Archimycetes and associated groups, and possibly the Actinomycetes, whose conceivable relation to certain fungi has not yet, in my opinion, received adequate consideration.

Alexopoulos (1952) recognizes that there is a strong and growing opinion among mycologists that the fungi may have originated from animal-like forms, but remarks, "Since we admit of only two kingdoms . . . and since the fungi are more in agreement with our concept of plants than of animals, we classify them in the plant kingdom regardless of personal belief about their ancestry." This is probably as accurate a statement of the predominant attitude at the present time as could be made. It does, however, beg the question of the origins and validity of "our concept of plants" and, as carried into practice, it tends to petrify preconceptions.

I am not suggesting that the fungi be withdrawn from the field of

botany in the wide sense. That would be impracticable at the present time for many reasons. In the field of classification, for example, there is no reason why mycologists should not work within the frame of the International Code. It is true that provisions made primarily by phanerogamists for phanerogams are not always adaptable to the fungi, but the phanerogamists have been perfectly willing to recognize that fact. When the Vienna rules were adopted, the provision of special starting points for the fungi was made at the behest of the mycologists (most unfortunately, it seems to me, particularly in the case of the gasteromycetes) and when at Stockholm, in 1950, recommendations were adopted looking toward standardization of names of groups above the rank of order, the mycologists on the committee recommended unanimously that the divisional name for fungi should end in *-mycota* rather than *-phyta*, with the corresponding *-mycotina*, *-mycetes*, and *-mycetidae* for subordinate groups. This was adopted by the Congress and incorporated as Recommendation 26A in the Code. At the same time the use of the imperfect name for the imperfect stage of a fungus where the perfect stage is known—a matter of great practical importance to mycologists—was formally validated by amendment to Art. 69. So long as this spirit of accommodation prevails, there need be no difficulty about treating the fungi with plants for purposes of nomenclature.

In a more general way, fungi will continue to be discussed in botanical texts and studied, for the most part, in botanical laboratories or as part of the botanical sequence in biological courses, just as bacteria are. There is no reason, however, why in this, or in any other connection, theory should be stated as fact.

I said at the beginning that I did not intend to answer the question I have posed, nor have I attempted to analyze in detail the arguments which have been advanced for the derivation of the fungi from the algae. These arguments are on record and must be considered seriously and objectively. I have raised the question whether we have not allowed ourselves to be hampered in our thinking by certain long-established beliefs which have become so deeply entrenched that we have taken their validity for granted and that we have consequently failed to disentangle them from our appraisal of the facts we know. The use of the term "plant" for fungus carries within itself such a preconception and this is intensified by the use of suffixes such as *-phyta* to designate groups of fungi. The belief that all living things must be either plants or animals has the authority of antiquity behind it, but little else. The belief that green plants must have preceded animals and fungi is, at most, a pious belief rather than a demonstrated fact. The impossibility of

drawing a line between what were called plants and what were called animals has been increasingly recognized for over three-quarters of a century. At the present time, the line between living and non-living is becoming correspondingly vague. It is now necessary to postulate that whenever and wherever life may have originated, conditions on the earth's surface, including its atmosphere, may have been very different from what they are now. It is at least permissible to question whether the chemical combinations which had within them the potentialities for living processes may not have originated at different times and places and in different form. The best way to recognize this viewpoint, so far as the fungi are concerned, is to treat them in the same way that Smith treats the algae. The exact limits of the fungi, the number of developmental lines to be recognized, the inclusion or exclusion of specific groups: these are all matters on which there will be legitimate difference of opinion for a long time to come. But our approach to these problems will, in my opinion, be greatly facilitated if we remove the road-blocks which hamper our progress.⁴

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⁴ I am grateful to Dr. Donald P. Rogers for reading this paper at the East Lansing meeting, which I could not attend because of illness. After it had gone to the printer, Dr. Rogers sent me a quotation from D. H. Scott: *Flowerless plants*, 12th ed., revised by C. T. Ingold. London. 1955, p. 122: "The old view that Fungi have arisen from algal ancestors is now supported by few authorities, and indeed, many students of Fungi consider that they should be classified in a separate kingdom of living organisms." This may be true of the mycologists of the Old World, but it is my impression that in the Americas, those who hold such a view are in a decided minority.

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THE CARDINAL TEMPERATURES AND pH RESPONSE OF THIELAVIOPSIS BASICOLA¹

G. B. LUCAS

(WITH 1 FIGURE)

The severity of black root rot of tobacco, caused by *Thielaviopsis basicola* (Berk. and Br.) Ferr., is influenced markedly by soil temperature and pH. Field studies by Johnson and Hartman (5) indicated the occurrence of the disease is determined primarily by soil temperature. Valleau *et al.* (11) reported that black root rot injured tobacco in the field at 21–23° C, but above 25.5° C the host grew fairly well and the disease caused little damage. It is also well established (3) that black root rot is more severe on soils which have a pH of 6.0 or above.

To gain a better understanding of the effects of soil temperature and pH on black root rot, various workers have studied the causal organism in culture and used greenhouse inoculation tests under controlled conditions. The optimum temperature for growth of the pathogen in culture has been reported to be 28–30° C; these temperatures are also favorable for growth of the host (1, 4, 5, 6). Rawlings (8) studied the influence of temperature and pH on the growth of *T. basicola* cultures obtained from tobacco in Tennessee, cotton in Texas and *Primula obconica* Hance in Holland. When cultured on potato-dextrose-agar at 10, 20 and 30° C, all isolates grew most rapidly at 20° C and growth was faster at 10° C than at 30° C. When grown on potato-dextrose-agar adjusted to pH 4, 5, 6, 7 and 8, all isolates grew faster at pH 6, 7 and 8 than at 4 or 5. In 1950 Steinberg (9) demonstrated that calcium was an essential minor element for the growth of *T. basicola* in synthetic nutrient solutions. However, increasing the calcium level above 2 ppm did not increase the yield of mycelium. Steinberg (personal communication) also found that growth (dry weight) in synthetic media was least at 20° C, intermediate at 23° C and most at 30° C. On the other hand Barnett *et al.* (1) reported that growth was more rapid at 25° C than at 20, 30 or 31.5° C.

¹ Contribution from Plant Pathology, North Carolina Agricultural Experiment Station, Raleigh, North Carolina. Published with the approval of the Director of Research as Paper No. 639 of the Journal Series.

Johnson and Hartman (5) showed that black root rot was most severe at temperatures ranging from 17 to 23° C, much less severe at 26° C and negligible at 30° C or above. Doran (2) found that pH influenced the effect of temperature on black root rot development, the critical pH range being between 5.6 and 6.0. At pH 5.6 or below, the disease did not develop at any temperature. However, as the pH was raised to 5.7, 5.7-5.8, 5.8 and 5.8-5.9, the highest temperatures at which black root rot developed were 15, 18, 21 and 27° C, respectively. There was little or no disease development at 30° C in soils with pH levels ranging from 6.0 to 6.9. In the light of these results Walker (12) cited black root rot of tobacco as a disease which is favored by temperatures that are not optimum for growth of either the pathogen or the host.

In preliminary studies, isolates of *T. basicola* from North Carolina appeared to have temperature optima for growth in culture below the 28-30° C range previously reported. Therefore, additional studies on the cultural behavior of the fungus was undertaken.

This paper reports data on 1) the cardinal temperatures of certain isolates of *T. basicola*, 2) the growth of these isolates on buffered media adjusted to different hydrogen ion concentrations and 3) the interaction of excess calcium ions and pH on growth.

MATERIALS AND METHODS

Cultures of *T. basicola* from Kentucky, Wisconsin, Virginia and California, obtained through the courtesy of Drs. W. D. Valleau, R. W. Fulton, R. G. Henderson and C. E. Yarwood, respectively, and 1 from North Carolina were used. All isolates were the gray type, according to Stover's (10) classification, and all were pathogenic to tobacco.

Temperature Studies. The effect of temperature on growth was determined by incubating the cultures in controlled temperature cabinets at 4° (± 1) intervals from 8 to 36° C and also at 22, 26 and 30° C. Oatmeal agar (200 gms oatmeal per l of water, pH approximately 6.6 after autoclaving) in Petri plates was seeded with disks of mycelium, 1 mm in diameter, from the margin of a 1-week old colony. Usually 3 plates of each isolate were incubated at each temperature and all isolates were tested in at least two different tests. Growth rates were determined by measuring colony diameter at intervals from the fourth to the fourteenth day. In addition, all the isolates, with the exception of the North Carolina isolate, were grown at least once in potato-dextrose-broth

at 4° intervals from 20 to 32° C. After 5–14 days of growth the cultures were filtered and the mycelial mats were air dried and weighed.

Hydrogen Ion Studies. The effect of pH on growth was determined by growing the fungus in potato dextrose broth (extract from 200 gms potatoes plus 17 gms dextrose per l of water). To each 35 ml aliquot of sterilized broth 2 ml of sterilized buffer (1.3 gms citric acid, 1.9 gms glycine, 1.9 gms monobasic potassium phosphate per 50 ml of water) were added aseptically. The resultant pH was approximately 4.0. Using normal hydrochloric acid or sodium hydroxide, the pH was adjusted at intervals of 0.1–0.5 from pH 2.8 through pH 9.0. Duplicate flasks were seeded with the Virginia, Wisconsin and Kentucky isolates by adding 2 drops of a conidial suspension to each flask. The cultures were incubated at room temperature or at 24° C for 12–14 days before the mycelial mats were removed by filtering, dried and weighed, and the final pH of the filtrates was determined with a Beckman pH meter.

Additional tests were conducted with the North Carolina and Wisconsin isolates using a liquid synthetic medium (50 gms sucrose, 4 gms asparagine, 2 gms dibasic potassium phosphate, 0.3 gms magnesium sulfate, 20 ml normal calcium chloride, 1 mg ferric nitrate and 1 mg thiamin chloride per 1000 ml of water) which was buffered to a pH of approximately 5.8 with a buffer similar to the one described above. Titration to pH intervals, inoculation, incubation conditions and evaluation were as previously described. Another test including all 5 isolates was similarly conducted using the unbuffered synthetic medium described above, adjusted to pH values from 3.0 to 8.7.

Calcium Ion Studies. Excess calcium ions were provided by adding 0.5 ml, or approximately 300 ppm, of normal calcium chloride to each of a series of flasks containing 35 ml of buffered potato-dextrose-broth or the synthetic medium and the pH adjusted from pH 2.8 through 9.0. Similar media, without the calcium chloride, were used as controls. Inoculation, cultural conditions and evaluation were as described for the preceding tests.

RESULTS

Measurements of colony growth of 5 isolates of *T. basicola* are shown graphically in FIG. 1. For each isolate, the colony diameters shown represent the average of three trials. None of the isolates grew at 8° C or at 36° C. Each grew well at temperatures ranging from 22 to 28° C with an average optimum of about 26° C. In potato-dextrose-broth, mycelial mat weights after 8 days growth at 20, 24, 28, 30 and 32° C averaged 77, 80, 50, 26 and 10 mg, respectively.

The growth responses for the Virginia, Wisconsin and Kentucky isolates to pH in buffered potato-dextrose-broth were quite similar. No growth occurred below pH 3.3 or above 7.2 and the optimum pH range for growth was between 3.9 and 6.2. In the presence of excess calcium (approximately 300 ppm) in potato-dextrose-broth slight growth occurred at pH 3.0 and mycelial mat weights were greater over the pH range than in potato broth without excess calcium.

When all 5 isolates were grown in the unbuffered synthetic medium without excess calcium, no growth occurred below pH 3.3 and maximum

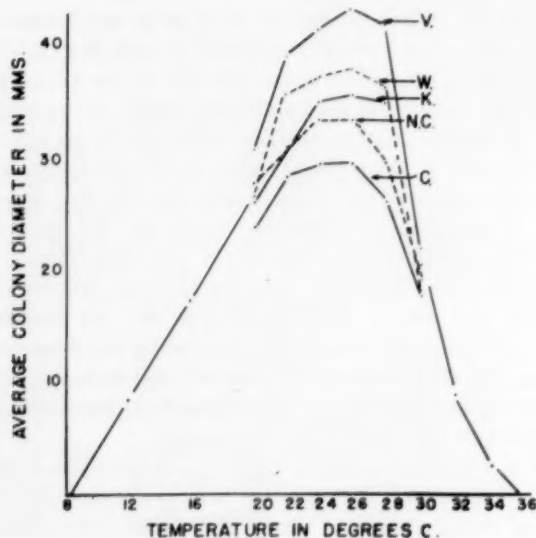


FIG. 1. The effect of temperature on the growth of *Thielaviopsis basicola* on oatmeal agar. The graph represents 6 days' growth from an average of 3 trials of 5 isolates from widely scattered areas.

growth occurred from approximately 4.4 to 6.4. Some growth occurred in flasks at an initial pH of 8.7. However, at the end of 14 days the pH in these flasks varied from 6.1 to 6.8.

In the buffered synthetic medium the Wisconsin and North Carolina isolates produced little or no growth below pH 3.0 or above 8.0 and optimum growth occurred from approximately 4.0 to 6.4. When excess calcium was added to the medium the mycelial mat weights were greater over the pH range than were those of the mats obtained from the basal medium.

DISCUSSION

Temperature Requirements. It is well known that races of *T. basicola* occur in nature (10). It is entirely possible that both Gilbert (4) and Johnson and Hartman (5) studied strains of the fungus whose optimum temperature for growth was 28–30° C. Whether or not these strains are representative of the fungus as it occurs in nature is another question. It appears significant that the 3 isolates tested by Rawlings, obtained from 3 different hosts from 3 widely separated locations, grew faster at 20° C than at 30° C. Add to this the 5 isolates herein studied from California (from bean), Wisconsin, Kentucky, Virginia and North Carolina (from tobacco), all of which grew about equally well at temperatures between 22 and 28° C, and there is strong evidence that strains of the fungus, widely distributed in nature, have optimum temperature ranges for growth extending well below 28° C.

It would appear, then, that black root rot of tobacco is a disease which is most severe at temperatures which extend into the optimum range for the parasite but not for the host.

Hydrogen Ion Requirements. No reports were found in the literature in which buffered media were used to determine the effect of hydrogen ion concentration on growth of *T. basicola*. It is well known (7) that the pH of media may change considerably after several days of microbial growth. Rawlings' (8) results of rapid growth at pH 6.7 or 8 might be explained by a shift to a lower pH. Rawlings did not mention pH determinations made at the end of the growth period.

Calcium Ion Effect. The addition of calcium to buffered potato-dextrose-broth permitted the fungus to grow at a lower pH than unfortified potato-dextrose-broth. Also the addition of excess calcium to both potato-dextrose-broth and a synthetic medium resulted in higher mycelial mat weights. Just how and why the addition of excess calcium produces the two effects noted above is not known.

The fact that black root rot is more severe on soils which have been limed or which have a pH of 6.0 or above cannot be explained by unfavorable pH effect only, for the optimum pH for fungus growth extends well below this value. Moreover, Doran (3) found when the pH of soil was lowered from 5.9 to 5.0 by the application of orthophosphoric acid, black root rot was "still severe or even more severe." Doran speculates that "orthophosphoric acid as well as lime inactivates toxic substances with consequent benefit to the fungus." It may be that excess calcium added to the medium inactivates certain enzyme systems or toxic ions and permits greater mycelial growth.

SUMMARY

On oatmeal agar, isolates of *Thielaviopsis basicola* from 5 widely separated areas had similar temperature-response growth curves. No isolate grew at 8° C. or at 36° C. Maximum growth for all isolates occurred between 22 and 28° C, contrary to previous reports of an optimum of 28–30° C. In buffered potato-dextrose-broth no growth occurred below 3.3 or above 7.2. Optimum growth occurred between pH 3.9 and 6.2. In the presence of excess calcium in potato-dextrose-broth the fungus grew sparsely at pH 3.0, and the mycelial mat weights were increased over cultures grown in medium lacking excess calcium and grown at comparable pH levels. In a buffered synthetic medium little or no growth occurred below pH 3.0 or above 8.0. The addition of excess calcium to this medium did not change these values but did increase the yield of mycelium.

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YEASTS ISOLATED FROM DROSOPHILA AND FROM THEIR SUSPECTED FEEDING PLACES IN SOUTHERN AND CENTRAL CALIFORNIA

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In 1948 Dobzhansky expressed the view that yeasts are important in understanding some of the forces of natural selection to which populations of *Drosophila* flies are exposed. Since then there has been an intense interest in the relation of yeast to *Drosophila* in nature. Although certain aspects of this relationship have been studied, information pertaining to the taxonomy of yeast occurring in *Drosophila* flies is quite limited.

Chatton (1913) reported the occurrence of *Coccidiascus ligeri* as an intestinal parasite of *D. funebris*. In 1944 Dobzhansky and Epling isolated a yeast, which they termed *S. farinosus* (syn. *Pichia farinosa*), from the crops of *D. pseudoobscura*. Later, at Dobzhansky's suggestion, Wagner isolated some yeasts from the crops of *D. pseudoobscura* collected at Pinon Flats in the San Jacinto mountains in Southern California. These were identified by Mrak (unpublished data) as species of the genus *Zygosaccharomyces*. Wagner (1944) also isolated but did not identify 8 types of yeast from *Opuntia* fruits and demonstrated that the yeasts had different nutritional qualities for certain species of *Drosophila*. Buzzati-Traverso in 1950³ isolated 15 cultures of *Torulopsis* from *Drosophila* flies trapped in the Po Valley in Italy. Hedrick and Burke (1950) and Hedrick and Burke (1952) identified 17 yeasts isolated from crop contents, feces, and immediate substrates of two species of flies (*D. crucigera* and *D. pilimana*) collected in Hawaii.

Shehata and Mrak (1952) compared the intestinal yeast floras of successive populations of *Drosophila*. In this study emphasis was placed on the relation of the type of yeast to the population cycles of the different chromosomal types of *Drosophila pseudoobscura* rather than on the taxonomy of the yeast isolated. In somewhat similar work da Cunha *et al.* (1951) demonstrated that certain yeasts isolated from the crops

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of *Drosophila* showed a differential attractiveness to certain species of *Drosophila*. Da Cunha (1951) also showed that the adaptive values of the different chromosomal structures in *D. pseudoobscura* vary, depending on the microorganisms used in the food of the flies and their larvae. Recently Dudgeon (1954) isolated 130 yeast strains from 21 species of *Drosophila*. The yeasts, which unfortunately were only identified by genus, fell primarily in *Debaryomyces*, *Hansenula*, *Pichia*, *Saccharomyces*, *Candida*, *Kloeckera* and *Torulopsis*. The 21 species of *Drosophila* (collected in 12 different states of the U. S.) showed no apparent preference for any of the genera of yeasts. Neither seasonal nor geographic variations in the genera of yeasts collected could be demonstrated.

The study reported in this paper was conducted in order to obtain more complete information on the taxonomic characteristics of yeasts occurring in *Drosophila* (particularly the *Obscura* group) flies collected in their natural mountain environment, and from various substrates (possible feeding places for the flies) in these environments.

EXPERIMENTAL PROCEDURE

Fly collections were made at Pinon Flats (a desert area) and Keen Camp, including Mountain Center (a yellow pine area), on Mt. San Jacinto in Southern California and at Mather and Jacksonville just northwest of Yosemite Park in central California. These areas were chosen because Dobzhansky and his colleagues had been collecting flies there for a number of years and because the variations in elevation and vegetation offered an unusual opportunity to consider yeast ecology.

Flies were collected, transported, dissected and identified according to the procedures described by Shehata and Mrak (1951, 1952). Taxonomic studies were originally made in accordance with the procedures of Stelling-Dekker (1931), Lodder (1934), and Diddens and Lodder (1942) but, upon the completion of these studies, newer and more useful procedures were published by Wickerham (1951) and Lodder and Kreger van Rij (1952). In order to avoid confusion the taxonomic studies were repeated in accordance with the newer procedures. Completion of the work, therefore, was delayed because of these circumstances. In conducting the studies reported in this paper the newer Dutch system was used insofar as possible; however, in a number of cases the Wickerham system had to be relied on for a more clear-cut species differentiation. As a result, some of the organisms originally listed by Shehata and Mrak (1952) as new species (based on Stelling-

Dekker's system) can now be identified with the modified descriptions of Lodder and Kreger van Rij (1952). In such cases it was decided not to describe these isolates as new species, even though there might still exist additional differences when using a much larger number of carbon compounds as recommended by Wickerham (1951) for the genus *Hansenula*. Organisms which do not fit in the Dutch system or in *Hansenula* as described by Wickerham will be proposed as new species. In these cases, the extended carbon assimilation patterns were used. In order to avoid a lengthy listing of all the assimilation reactions (both positive and negative) only the positive results are reported in the standard description of new species. All compounds recommended by Wick-

TABLE I
NUMBER OF ISOLATES OF VARIOUS GENERA

Genus	Source		Total
	Flies	Substrates	
<i>Saccharomyces</i>	60	3	63
<i>Candida</i>	19	23	42
<i>Kloeckera</i>	13	1	14
<i>Hansenula</i>	9	1	10
<i>Pichia</i>	3	7	10
<i>Torulopsis</i>	7	4	11
<i>Rhodotorula</i>	3	4	7
<i>Cryptococcus</i>	—	4	4
<i>Hanseniaspora</i>	2	2	4
<i>Trichosporon</i>	—	2	2
<i>Oospora</i>	2	—	2
	118	51	169

erham (1951) were used with the exception of D-glucosamine, pyruvic acid, ethylacetoacetate and potassium sodium saccharate.

EXPERIMENTAL RESULTS

A total of 169 cultures were isolated. One hundred and eighteen of these were obtained from *Drosophila* flies and 51 from substrates. The occurrence of yeast by genera is summarized in TABLE I and by species according to source and place of origin in TABLES II and III. The taxonomic treatment of these organisms is discussed below.

Genus *SACCHAROMYCES*: The 63 cultures of *Saccharomyces* isolated were identified as follows: *S. cerevisiae* Hansen (26), *S. veronae* Lodder & van Rij (18), *S. fragilis* Jørgensen (6), *S. fermentati* (Saito) Lodder

& van Rij (2) and three new species, *S. drosophilorum* (10), *S. dobzhanskii* (1) and *S. phaselosporus* (1).

The isolates now termed *S. veronae* were originally considered *S. drosophilae* (Shehata & Mrak, 1952). After the publication of the

TABLE II
YEASTS ISOLATED FROM FLIES COLLECTED IN DIFFERENT AREAS

Genus and Species	Geographical location where flies were collected				Total
	Pinon Flats	Keen Camp Area	Jacksonville	Mather	
<i>Saccharomyces cerevisiae</i>	13	10	2	1	26
<i>Saccharomyces veronae</i>	3	12	2	1	18
<i>Saccharomyces drosophilorum</i>		6		1	7
<i>Saccharomyces fragilis</i>	6				6
<i>Saccharomyces dobzhanskii</i>	1				1
<i>Saccharomyces phaselosporus</i>	2				2
<i>Candida krusei</i>	4	1			5
<i>Candida pulcherrima</i>	4				4
<i>Candida lipolytica</i>	2			1	3
<i>Candida parapsilosis</i>	2				2
<i>Candida rugosa</i>		1			1
<i>Candida mycoderma</i>		1		1	2
<i>Candida guilliermondii</i>	1				1
<i>Candida tropicalis</i>				1	1
<i>Kloeckera apiculata</i>	3	8		2	13
<i>Hansenula angusta</i>		6	1	2	9
<i>Hanseniaspora valbyensis</i>				2	2
<i>Torulopsis fermentans</i>	1		3		4
<i>Torulopsis bacillaris</i>	1				1
<i>Torulopsis colliculosa</i>	1				1
<i>Torulopsis aerea</i>	1				1
<i>Pichia membranaefaciens</i>	1	1		1	3
<i>Rhodotorula mucilaginosa</i>				1	1
<i>Rhodotorula glutinis</i>	1				1
<i>Rhodotorula aurantiaca</i>	1				1
<i>Oospora lactis</i>	1	1			2
Total Number of Yeasts Isolated	49	47	8	14	118
Number of Species Isolated	19	9	4	11	23
Number of Flies Yielding Yeast	37	37	7	11	92
Number of Flies Cultured	68	85	20	14	187
Number of Fly Collections Made	4	4	1	1	10

description of *S. veronae* by Lodder and van Rij (1952) it was apparent that these species were very similar. In view of this, an authentic culture of *S. veronae* was obtained from the C. B. S. collection in Holland and the complete carbon assimilation pattern was compared with that of representative isolates from flies. The results were so similar that there

TABLE III
YEASTS ISOLATED FROM VARIOUS SUBSTRATES IN DIFFERENT LOCATIONS

Genus and Species	Geographic location				Total	Materials from which yeasts were isolated
	Pinon Flats	Keen Camp	Jacksonville	Mather		
<i>Candida pulcherrima</i>		1	2	4	7	rotting wood, injured oak, rhamnus berries, slime flux
<i>Candida parapsilosis</i>	1	3	1		5	injured oak, injured pine, soil, onion & cactus flowers
<i>Candida mycoderma</i>				4	4	slime flux of <i>Q. kelloggii</i>
<i>Candida clausenii</i>		3			3	decaying wood
<i>Candida zeylanoides</i>				2	2	slime flux of <i>Q. kelloggii</i>
<i>Candida catenulata</i>		1			1	decaying wood
<i>Candida krusei</i>			1		1	lichen
<i>Pichia membranaefaciens</i>	1	4		2	7	injured pine, slime flux, cactus
<i>Cryptococcus albidus</i>	2				2	pine exudate, cactus
<i>Cryptococcus diffluentis</i>	1	1			2	onion flower, rhizome of yucca
<i>Torulopsis aeria</i>	3				3	cactus, pine exudate
<i>Torulopsis gropengiesseri</i>		1			1	grass
<i>Rhodotorula glutinis</i>	2				2	manzanita berries, juniper berries
<i>Rhodotorula glutinis</i> var. <i>rubescens</i>	1				1	pine exudate
<i>Rhodotorula mucilaginosa</i>	1				1	oak exudate
<i>Saccharomyces fermentati</i>		2			2	injured pine
<i>Saccharomyces drosophilae</i>		1			1	insect infested leaf of shrub
<i>Hanseniaspora uvarum</i>	2				2	juniper berries
<i>Trichosporon fermentans</i>				2	2	slime flux of <i>Quercus kelloggii</i>
<i>Hansenula angusta</i>				1	1	slime flux of <i>Q. kelloggii</i>
<i>Kloeckera apiculata</i>		1			1	bark beetle larva
Total Number of Yeast Isolated	14	18	4	15	51	
Number of Species Isolated	9	10	3	6	21	

is no doubt about the identity of the cultures. Besides the carbon compounds listed by Lodder and van Rij, the following assimilation characteristics are typical for this species: positive for L-sorbose, trehalose, raffinose, melezitose, ethanol (some strains latent), glycerol, D-mannitol, D-sorbitol, α -methyl-D-glucoside, L-arabinose (weakly assimilated) and gluconic acid and succinic acid (variable). The other compounds tested

are not assimilated. Lodder and van Rij (1952) reported that *S. veronae* is unable to use ethanol as the single source of carbon. We were unable to confirm this, since the type species grows in alcohol as well as our own isolates, which showed positive or latent growth.

The isolates termed *S. drosophilarum* are yeasts with kidney-shaped ascospores. Lodder and van Rij (1952) list only two species with such ascospores, *S. marxianus* and *S. fragilis*. Our cultures differ from both described species in assimilation and fermentation reactions, as well as in morphological characteristics. None of the cultures ferment lactose, which excludes them from *S. fragilis*. Furthermore, all cultures assimilate maltose and none assimilate lactose, separating them from *S. marxianus*. Other differences are the absence of a typical pseudomycelium and the smaller cells in malt extract. Since Stelling-Dekker (1931) did not use assimilation reactions or pseudomycelium characteristics, the cultures were originally classified as *S. marxianus*. However, the more extensive information now available justifies the description of a new species. The specific name *drosophilarum* was chosen since this yeast when used as bait (Phaff *et al.*, 1955) was highly attractive to a large number of different species of *Drosophila*. Representatives of this species have been isolated from *Obscura* group flies and in one case from leaves of a shrub infected with a lepidopterous insect in the Keen Camp region of Southern California and also from *Obscura* flies and a slime flux of *Quercus kelloggii* near Mather in the Central California Mountains.

Saccharomyces drosophilarum sp. nov.

In musto maltato cellulae ovoideae, $1.9-5.4 \times 2.3-6.7 \mu$, singulae, binae aut catenatae; sedimentum et anulus formatur. In agaro maltato cultura albida, plerumque glabra, mollis, semi-nitida, margine glabro. Pseudomycelium nullum. Copulatio cellularum heterogamica et isogamica conformationi asci plerumque praecedit. Ascospores reniformes, 2-4 inasco. Fermentatio glucosi, galactosi, sacchari et raffinosi pro tertia parte. In medio minerali cum glucoso, galactoso, sorboso, maltoso, saccharo, cellobioso, trehaloso, raffinoso, melezitoso, alcohole aethylico, alpha-methylglucosido crescit. Nitras kalicus non assimilatur.

Growth in malt extract: after 3 days at room temperature cells short oval, $1.9-5.4 \times 2.3-6.7 \mu$; single or in pairs and small chains. A ring and a sediment form gradually, but no pellicle. Streak culture on malt agar: greyish to cream-colored, surface semi-glistening and nearly smooth with many fine transverse striations, pasty texture, low convex cross-section, little-spreading with a lobulate margin. Slide cultures on potato dextrose agar: extremely primitive or no pseudomycelium. Sporulation abundant on wort agar. Iso- or heterogamic conjugation usually precedes ascus formation. Ascospores kidney-shaped, usually 4 per ascus.

The asci rupture readily at maturity. Fermentation positive for glucose, galactose, sucrose, and raffinose (one third only). Maltose and lactose not fermented. The following carbon compounds are assimilated: glucose, galactose, L-sorbose, maltose, sucrose, cellobiose, trehalose, raffinose, melezitose, ethanol, glycerol, D-mannitol, D-sorbitol, α -methyl-D-glucoside, salicin and lactate. Latent or variable assimilation occurs with D-xylose, succinate and citrate. The other compounds are not assimilated. Usually very thin dull pellicles are formed on assimilation media. Assimilation of nitrate negative. Vitamins are required for growth in a synthetic medium. Starch-like compounds are not synthesized.

Another isolate was a yeast with kidney-shaped ascospores, which could not be identified with existing species. It resembles *S. drosophilae* in carbon assimilation pattern, but differs in its ability to cause a strong fermentation of maltose. It is, therefore, considered to be a new species, for which we propose the name *Saccharomyces dobzhanskii* in honor of Professor Th. Dobzhansky, who stimulated the study of yeasts associated with *Drosophila* flies. A single isolate was obtained from *D. pseudoobscura* collected at Pinon Flats in Southern California.

Saccharomyces dobzhanskii sp. nov.

In musto maltato cellulae ovoidae aut rotundae, $2.0-6.0 \times 2.7-7.0 \mu$, singulae, binae aut catenatae; sedimentum et anulus formantur. In agaro maltato cellulae copulantes et asci. Cultura albida, mollis, glabra. Pseudomycelium nullum. Ascosporae reniformes, 2-4 in asco. Copulatio cellularum heterogamica et isogamica conformationi asci plerumque praecedit. Fermentatio glucosi, galactosi, sacchari, maltosi et raffinosi pro tertia parte. In medio minerali cum glucoso, galactoso, sorboso, maltoso, saccharo, cellobioso, trehaloso, raffinoso, melezitoso, alcohole aethylico, alpha-methylglucosido crescit. Nitras kalicus non assimilatur.

Growth in malt extract: after 3 days at room temperature cells oval to spherical, $2.0-6.0 \times 2.5-7.0 \mu$, single, in pairs, or in small chains. Sediment and a ring are formed. Streak culture on malt agar: periphery white to cream-colored with a pinkish color along the center, surface nearly smooth with a few small warts and radial sectors, semi-glossy, soft, broadly convex, but not spreading, border entire. No pseudomycelium on potato dextrose agar slides. Sporulation abundant on wort agar. Iso- or heterogamic conjugation usually precedes ascospore formation. Asci rupture readily at maturity, releasing four kidney-shaped ascospores. Fermentation positive for: glucose, galactose (latent and weak), sucrose, maltose, and raffinose ($\frac{1}{3}$ only). Lactose not fermented. The following carbon compounds are assimilated: glucose, galactose, L-sorbose (may be latent), maltose, sucrose, cellobiose, trehalose, raffinose, melezitose, L-arabinose (variable), ethanol, glycerol,

D-mannitol, D-sorbitol, α -methyl-D-glucoside, salicin, gluconic acid (variable), lactic acid (latent to strong), succinic acid, citric acid (latent or -). The other compounds are not utilized. Nitrate not assimilated. Vitamins are required for growth in a synthetic medium. Starch-like compounds not synthesized.

Two other yeasts with kidney-shaped ascospores could not be identified with existing species. Both were isolated from *D. pseudoobscura* at Pinon Flats. In their fermentation characteristics they resemble *S. drosophilae*, but the assimilation pattern of carbon compounds is entirely different. Among these differences is the inability to assimilate maltose. The absence of lactose assimilation differentiates them from *S. marxianus*. Besides there are morphological differences, such as the absence of pseudomycelium. One of the isolates was originally considered as *Z. marxianus* (Shehata and Mrak, 1952) and the other isolate was tentatively designated as *Z. mrakii*. (See Shehata and Mrak, 1952.) To avoid confusion both isolates will be described as *Saccharomyces phaselosporus* nov. spec. because of the formation of ascospores resembling kidney beans.

***Saccharomyces phaselosporus* sp. nov.**

In musto maltato cellulae subovoideae, $2.1-5.3 \times 2.6-6.3 \mu$, singulae, binae aut breviter catenatae, pellicula non formatur. Cultura in agaro maltato flavalbida, mollis, glabra, nitida, margine glabro. Pseudomycelium nullum. Ascosporae reniformae, 2-4 in asco. Copulatio cellularum aequarum conformationi asci plerumque praecedit. Fermatio glucosi, galactosi, sacchari, raffinosi pro tertia parte. In medio minerali cum glucoso, galactoso, sorboso, saccharo, raffinoso, xyloso (exiguo), alcohole aethylico (exiguo), glycerole, mannitole, sorbitole crescit. Necessariae ad crescentiam sunt vitaminae externae.

Growth in malt extract; after 24 hours or 2 days cells oval, $2.1-5.3 \times 2.6-6.3 \mu$, single, in pairs and in short chains. A poorly developed ring develops gradually, but no pellicle. Growth on malt agar: after 3 weeks the streak culture is cream-colored, smooth, with a delicately transverse striation on the periphery, glistening, pasty to soft, cross-section low convex, border lobulate without pseudomycelium. On potato dextrose agar slides no pseudomycelium is formed. Sporulation after isogamic conjugation. Usually 4 kidney- to crescent-shaped ascospores are formed in each ascus, which ruptures at maturity. Glucose, galactose, sucrose and one-third of raffinose are fermented. Maltose and lactose not fermented. Assimilates glucose, galactose, L-sorbitol, sucrose, raffinose, xylose (latent), ethanol (latent), glycerol, mannitol, sorbitol, salicin, sodium lactate (latent) and sodium succinate (latent). The other carbon compounds tested are not assimilated. Potassium

nitrate not assimilated. Requires vitamins for growth in a synthetic medium. Starch-like compounds not synthesized. Weak acid production on chalk agar.

All other isolates of *Saccharomyces* could be identified by the system of Lodder and van Rij.

Genus HANSENIASPORA: Two cultures were originally classified as *Hanseniaspora melligeri* Lodder 1932. Later Lodder and van Rij (1952) decided that this species was identical with *Hanseniaspora valbyensis* Kloecker 1912, with which we concur. Two other cultures were termed *Kloeckeraspora apiculata* (Lindner) Dvornik in our earlier paper, because of the presence of one or two spherical ascospores per ascus. Lodder and van Rij (1952, p. 309) studied two species of this genus, which they obtained from Niehaus, who established the genus (1932). The species, *Kloeckeraspora uvarum* and *Kloeckeraspora osmophila*, were provisionally included in the imperfect genus *Kloeckera*, as *Kloeckera apiculata* and *Kloeckera magna* respectively, because Lodder and van Rij were unable to observe sporulation in the two strains and the original spore description was not convincing to them. Mrak and Phaff (1948) also pointed out the controversial nature of the ascospores of *Kloeckeraspora*. Since that time a considerable number of abundantly sporulating strains have been isolated in our laboratory and we now feel certain that the spherical bodies in question are true ascospores. However, in line with the suggestion made by Mrak and Phaff (1948), we prefer to include these yeasts in the genus *Hanseniaspora*. Since the present isolates ferment only glucose and assimilate only glucose (of the sugars used in the Dutch System) the proper name is *Hanseniaspora uvarum* (Niehaus) comb. nov.

Genus HANSENULA: Ten cultures have been included in *H. angusta* Wickerham. These bear a certain similarity to *S. pastori* as described by Stelling-Dekker (1931) except for the utilization of nitrate. Until the positive utilization of nitrate became apparent these organisms were included in *S. pastori* by Shehata and Mrak (1952).

Genus PICHIA: Ten cultures were isolated and originally listed as 4 distinct species, including two species described as new, *P. bisporea* and *P. mrakii*. In line with the newer taxonomy, however, all isolates have been combined into *P. membranaefaciens* Hansen.

Genus CANDIDA: The 42 cultures included in the genus *Candida* fit well into the designated species (see TABLES II and III). It was, however, necessary to change the names of certain organisms classified under the older system. Specifically these were: *C. krusei* var. *vanlaeriana* and *Mycoderma vini* to *Candida mycoderma* (Reess) Lodder

& van Rij, and *C. monosa* to *Candida krusei* (Cast.) Berkhout. The organisms originally considered as the new species *C. pseudoalbicans* have since been described independently by the Dutch workers as *Candida clausenii* Lodder & van Rij (1952).

GENUS KLOECKERA: Thirteen cultures originally designated as *K. lindneri* are now included in the species *K. apiculata* (Reess emend. Kloecker) Janke. They appear to be imperfects of *H. valbyensis*.

GENUS TORULOPSIS: Eleven cultures were identified as follows: *T. fermentans* Mrak & McClung (4), *T. aerea* (Saito) Lodder (4), *T. groppengiesseri* (Harrison) Lodder (1), *T. bacillaris* (Kroemer & Krumbholz) Lodder (1), and *T. colliculosa* (Hartmann) Saccardo (1).

The revised taxonomy has resulted in a number of changes from that originally used by Shehata and Mrak (1952). A new species, namely *T. granulosa*, and a new variety, *T. granulosa* var. *nitida*, were there listed. These have both been included in *T. aerea* because of the close similarity. While there are slight differences, they are not sufficient to justify the retention of either a new species or a variety. Other revisions include the following changes: *T. rugosa* and *T. rugosa* var. *fermentans* which were indicated as new species and varieties have been included in *Candida parapsilosis* (Ashf.) Langeron & Talice because of the observation of pseudomycelia due to the use of more sensitive techniques. *T. pulcherrima* and *T. pulcherrima* var. *variabilis* have been changed to *Candida pulcherrima* (Lindner) Windisch.

GENUS CRYPTOCOCCUS: Two isolates belonging to this genus were identified as *Cryptococcus albidus* (Saito) Skinner, and two as *Cryptococcus diffluens* (Zach) Lodder & van Rij. In the original paper *Cr. albidus* was described as *Torulopsis albida* and *Cryptococcus diffluens* as *Torulopsis rotundata*.

GENUS RHODOTORULA: Seven cultures of *Rhodotorula* were isolated from various sources. The original taxonomic designations required but one change, *R. mucilaginosa* var. *carboni* to *R. mucilaginosa*.

GENUS TRICHOSPORON: The identity of two cultures of *Trichosporon fermentans* Diddens & Lodder was confirmed. Two isolates corresponding to *Gespora lactis* were also obtained from flies.

DISCUSSION

About one-half the cultures isolated from flies were representatives of the genus *Saccharomyces*. Since each isolate listed was obtained from a different fly, the total number of *Saccharomyces* isolates represents 60 different flies from the four different locations in California.

While a fair number of the *Saccharomyces* obtained were included in *S. cerevisiae*, the authors cannot be absolutely certain of the presence of typical bakers yeast (*S. cerevisiae*) in nature. Although the traps, containing a banana mash fermented by bakers yeast, were covered with a fine screen, it is virtually impossible to guarantee that none of the flies was able to reach a particle of the bait. In addition, during an extended survey of yeasts associated with *Drosophila* in Central California, typical bakers yeasts were never isolated when using a bait in which the yeasts were killed by exposure to ethylene oxide (Phaff, 1955).

It is significant that a large number of the cultures of *Saccharomyces* had haploid vegetative cells, and as a result would have been included in *Zygosaccharomyces* in the older taxonomic systems. The findings show that yeasts belonging to the genera *Saccharomyces*, *Kloeckera* (and its perfect form *Hanseniaspora*) and *Hansenula* were much more common in flies than in the possible feeding substrates investigated. Several species, in fact, were isolated only from flies (see TABLES II and III). Conversely, certain organisms such as *Trichosporon fermentans*, the species of *Cryptococcus* and certain species of *Candida*, were isolated only from natural substrates. In a limited number of cases certain species of yeasts were isolated from both flies and substrates. The most significant observation is that certain yeasts which were relatively abundant in flies were not isolated from substrates in the areas of collection. This means that the principal feeding places of the flies are still uncertain. On the other hand, it cannot be assumed in cases where certain yeasts were isolated from both flies and substrates that the natural feeding substrate definitely has been established.

Our present survey was very broad and intended primarily to obtain clues for further and more intensive studies, particularly with regard to natural substrates as specific habitats for certain yeasts. While it has been established that certain flies breed in slime fluxes (Carson, 1951), our findings indicate that it is uncertain whether flies in nature feed on these or other substrates studied. The observation of the rather common occurrence of certain species of *Saccharomyces* and the apiculate yeasts in the flies collected in various areas of California will be of value in guiding future studies designed to locate the feeding places of flies in nature. When the feeding places of the flies are discovered, the ecology of these groups of yeasts will also be better understood.

SUMMARY

1. One hundred and sixty-nine yeast cultures were isolated from flies and substrates collected in various areas in California. One hun-

dred and eighteen of these cultures were isolated from flies and fifty-one from substrates.

2. Most of the organisms isolated from flies belong to the genera *Saccharomyces*, *Candida*, *Kloeckera* and *Hansenula*, whereas most of those obtained from substrates belong to the genera *Candida* and *Pichia*.

3. Three new species of *Saccharomyces* (*S. drosophilorum*, *S. dobzhanskii* and *S. phaselosporus*) have been described. In these cases species designation has not only been based on the newer Dutch system of taxonomy but also on the utilization of additional carbon compounds according to the procedure of Wickerham.

ACKNOWLEDGMENTS

The authors are greatly indebted to Dr. L. J. Wickerham for counsel and assistance generously given in working out some of the difficult taxonomic problems involved in the preparation of this paper.

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CULTURAL AND INTERFERTILITY STUDIES IN *APORPIUM CARYAE*¹

RUTH MACRAE²

(WITH 21 FIGURES)

Among some specimens sent to the author for identification by Mr. K. A. Harrison of the Plant Pathology Laboratory at Kentville, Nova Scotia, was one collection from a poplar log along the Cannan Road, near Kentville, N. S. This fungus, with its resupinate growth habit and its pored hymenial surface, gave all the appearances of being a *Poria* but, on examination, was found to have the cruciate-septate basidia characteristic of the Tremellaceae.

Teixeira and Rogers (2) have observed cruciate-septate basidia, like those found in the Tremellaceae, in *Poria canescens* Karst., the type species of the genus *Aporpium* Bondarzew and Singer. They found that this fungus had been described under a number of different names but that the septate nature of the basidia had never been noted. They have redescribed the genus *Aporpium* as a genus in the Tremellaceae and have placed the fungus in that genus under the name *Aporpium caryae* (Schw.) Teixeira & Rogers. Their paper gives a full description of *A. caryae* and a discussion of its synonymy.

From the description of *A. caryae* in Teixeira and Rogers' paper, from an examination of a specimen of *A. caryae* determined by Dr. Rogers and loaned to the author by Dr. W. I. Illman of Carleton College, Ottawa, and from information given Dr. Rogers by Mr. K. A. Harrison about his collection, there is no doubt that the Kentville specimen belongs to this species.

The immature epibasidia in the Nova Scotia specimen have a characteristic stout, blunt appearance. The mature epibasidia are much larger than the sterigmata of the *Porias* but might sometimes be mistaken for them. The spores are allantoid and of a comparatively wide diameter. Similar "sterigmata" and spores had been noted previously in three specimens received for identification from the Forest Biology Laboratories at Victoria, British Columbia, and at Fredericton, New

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Brunswick. On closer examination, these three collections were seen to have the same cruciate-septate basidia as the specimen from Nova Scotia and to belong to the same species. A search through the Porias that were waiting identification at the Ottawa Laboratory revealed eleven additional collections of the fungus, making fifteen collections in all. Of these, two were found on *Betula lutea* Michx. and *Populus* sp. in Nova Scotia, three on *Populus tremuloides* Michx. and *Populus* sp. in Ontario, and ten on *Populus trichocarpa* Torr. & Gray ex Hook. and *P. tremuloides* in British Columbia. From two of the British Columbia collections, the Victoria Laboratory had sent cultures as well as sporophores. These cultures fruited and single spore isolates were obtained from the fruit bodies in both cultures. With this material at hand, an examina-



FIG. 1. Sporophore of *Aporpium caryae*, No. DAOM 31250, $\times 1$.

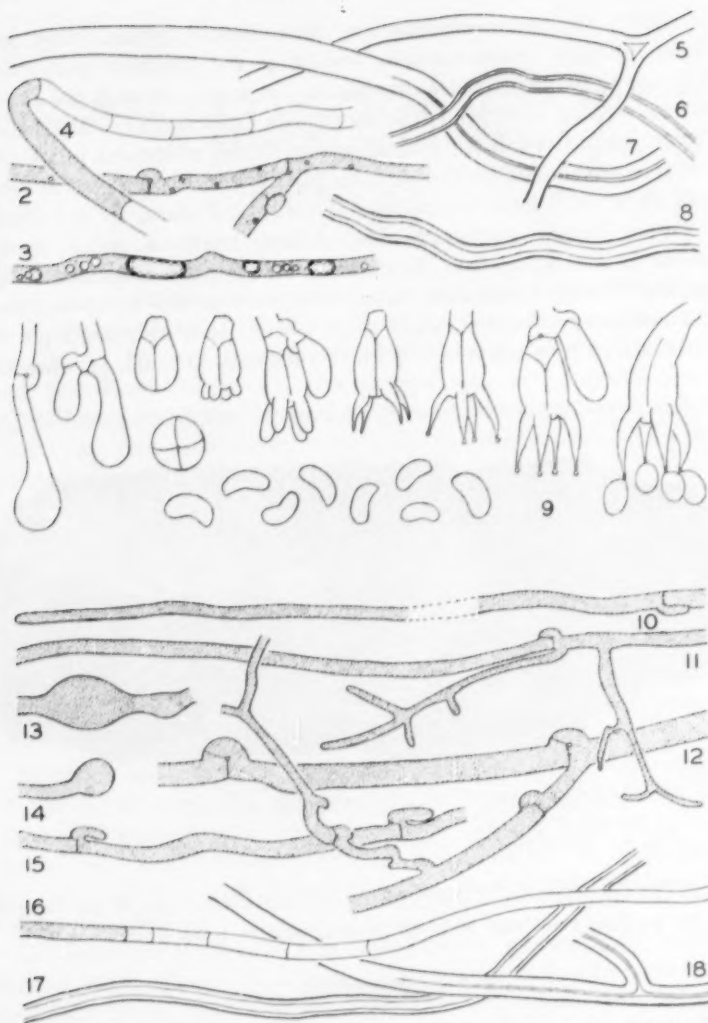
tion of the sporophores, a study of the cultural characters of the fungus, and the pairing reactions of single spore isolates were undertaken.

SPOROPHORES

A description of the specimen collected by K. A. Harrison on *Populus* sp., Cannan Road, near Kentville, N. S., follows (Figs. 1-9).

APORPIUM CARYAE (Schw.) Teixeira & Rogers

Resupinate, annual, not separable, pored, 10×3 cm, Light Pinkish Cinnamon (Ridgway) to Light Ochraceous Buff, Wood Brown when looking into the tubes, Sanford Brown and Auburn where bruised or



FIGS. 2-9. Hyphae, basidia, and basidiospores from a sporophore of *Aporidium caryae*, No. DAOM 31250. 2-4. Thin-walled hyphae showing clamp connections, oily contents, and simple septa formed by recession of cytoplasm. 5-8. Thick-walled hyphae. 9. Immature and mature basidia, end view of a basidium, and basidiospores. Complete septation could not be seen in the basidium on the right, $\times 1172$.

FIGS. 10-18. Hyphae from cultures of *Aporidium caryae*, No. DAOM 31251. 10-11. Hyphae from advancing zone, $\times 507$. 12-18. Aerial hyphae, $\times 1172$.

in older parts; margin thin, white, fimbriate, with pores forming to the edge; pores (1-)2-3 per mm, to 3 mm in length, angular, walls paper-thin, edges whitish, fimbriate; subiculum less than 1 mm thick, concolorous with the tubes; taste mild; context composed of a layer of closely interwoven hyphae continuous with the trama and, frequently, a narrow layer, 40-100 μ thick, next to the substratum, made up of closely parallel, thin-walled hyphae staining in phloxine; majority of hyphae thick-walled to solid, non-septate, unbranched or very rarely forked, 2.1-4.9 μ diameter; thin-walled hyphae also present, staining in phloxine, usually with scattered oil drops or empty of contents, frequently branched, nodose-septate, 1.4-2.8 μ diameter, occasionally simple septa seen in hyphae which have lost their contents, appearing to be formed as the cytoplasm recedes along the hypha; hyphal pegs present; cystidia none; hypobasidia ovate to pyriform, cruciate-septate, 4.9-7 μ diameter, with a basal cell cut off by the septation of the basidium and with a clamp connection at the base of this cell, the clamp connection best seen in immature basidia; epibasidia subulate to tubular, 5.6-9.8 μ long including the sterigma; spores hyaline, smooth, allantoid, non-amyloid, 5.3-6.3 \times 2.1-2.8 μ .

Specimens examined:

British Columbia: On *Populus tremuloides*, Six Mile Lake, Quesnel, W. G. Ziller, Aug. 6, 1949, ^aDAOM 31252 (DAVFP 5038); Silverton, W. G. Ziller, Aug. 19, 1950, DAOM 31260 (DAVFP 6695). On *Populus trichocarpa*, Cinema, W. G. Ziller, Aug. 15, 1949, DAOM 31251 (DAVFP 5125), DAOM 31253 (DAVFP 5130); Sept. 20, 1948, DAOM 31256 (DAVFP 3810), DAOM 31258 (DAVFP 3812); Aug. 11, 1949, DAOM 31255 (DAVFP 5083); Cottonwood, W. G. Ziller, July 18, 1949, DAOM 31254 (DAVFP 4928); Quesnel, W. G. Ziller, Sept. 13, 1948, DAOM 31257 (DAVFP 3811); R. W. Thomas and D. G. Podmore, Sept. 8, 1949, DAOM 31259 (DAVFP 5498).

Nova Scotia: On *Betula lutea*, Whycocomagh, V. J. Nordin, July 27, 1950, DAOM 31262 (FPF 59). On *Populus* sp., Cannan Road, near Kentville, K. A. Harrison, Nov. 26, 1952, DAOM 31250 (KAH 1850).

Ontario: On *Populus tremuloides*, Black Sturgeon Lake, J. T. Basham, Aug. 28, 1949, DAOM 31265 (FPT 3150). On *Populus* sp.,

^a DAOM—Department of Agriculture, Ottawa, Mycological Herbarium.

DAVFP—Department of Agriculture, Victoria, Forest Pathology Herbarium.

FPF—Department of Agriculture, Fredericton, Forest Pathology Herbarium.

FPT—Department of Agriculture, Maple, Forest Pathology Herbarium.

TRTC—Cryptogamic Herbarium, University of Toronto.

CCM—Carleton College Herbarium, Ottawa.

Denbigh, D. A. Quirke, Sept. 24, 1951, DAOM 31263 (FPT 3151); Marion Lake, near North Bay, D. A. Quirke, Sept. 15, 1951, DAOM 31264 (FPT 3152).

Florida: On *Quercus* sp., Rochelle Hammock, near Gainesville, R. F. Cain, Sept. 3, 1954, TRTC 30713 (CCM 451).

U. S. S. R.: As *Poria canescens* Karst., on *Abies alba*, A. Pilat, Aug. 1935, Ex Pilat Fungi Carpatici Lignicoli Exsiccati No. 244.

CULTURES

From two of the collections, Nos. DAOM 31251 and DAOM 31252, cultures as well as sporophores were received from the Forest Biology Laboratory at Victoria, B. C. One of these, No. DAOM 31251, was grown on sections of poplar branches which had been sterilized at 15 pounds steam pressure for 30 minutes and kept moist in flasks in the laboratory. The culture fruited and the sporophore produced was found to have the cruciate-septate basidia characteristic of *Aporpium caryae*.

The cultures from these two collections were grown in Petri dishes on malt agar and on malt agar to which gallic or tannic acid had been added, according to the methods described by Nobles (1). The description given here has the same form as the descriptions in Dr. Nobles' paper and a similar key pattern is assigned to the culture so that it may be fitted into her key for the identification of cultures of wood-rotting fungi.

APORPIUM CARYAE (Schw.) Teixeira & Rogers

KEY PATTERN: (1, 2) 1 1 1 7 2 2 2 (2, 3) 2 2.

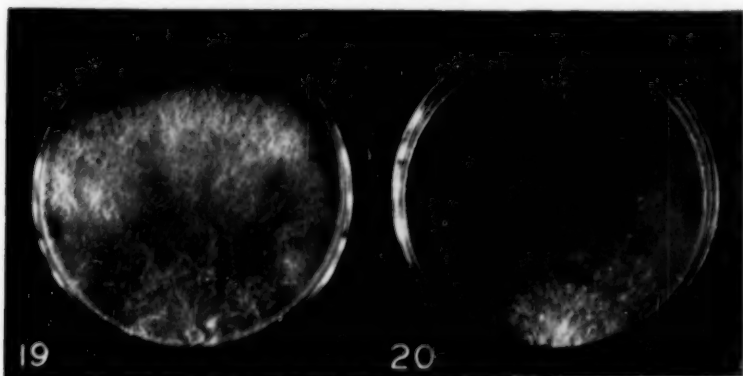
CULTURES EXAMINED: CANADA.—British Columbia: Cinema, on *Populus trichocarpa*, DAOM 31251; Six Mile Lake, Quesnel, on *Populus tremuloides*, DAOM 31252.

CULTURAL CHARACTERS (FIGS. 10-20)

GROWTH CHARACTERS.—Growth moderately rapid to slow, plates covered in four to six weeks. Advancing zone even, appressed, thin, individual hyphae distinct, a few raised, as seen under the dissecting microscope. Mat in culture No. 31251 white, thin, felty, thicker towards margin, with a narrow zone, about 5 mm in width, of thin, cottony mycelium around the inoculum; in No. 31252 white, thin, felty, becoming somewhat reticulate, raised at inoculum but appressed and finally translucent towards margin. Reverse unchanged. Aniseed odor.

On gallic and tannic acid agars diffusion zones very weak to weak, no growth.

HYPHAL CHARACTERS.—*Advancing zone*: hyphae thin-walled, hyaline, nodose-septate, with the completion of the clamp connection nearest the tip of the hypha usually considerably delayed, $2.1\text{--}4.2\ \mu$ in diameter, branches branching repeatedly. *Aerial mycelium*: (a) hyphae thin-walled, hyaline, nodose-septate, branched, $1.1\text{--}4.2\ \mu$ diameter, sometimes with a very short projection growing back from a clamp connection; (b) hyphae in some plates with occasional terminal or intercalary swellings to $11.9\ \mu$ diameter; (c) some hyphae with simple septa left when cytoplasmic contents have retreated along the hypha; (d) thick-walled, flexuous, non-septate hyphae present but not numerous, occa-



FIGS. 19, 20. Cultures of *Aporpium caryae*, three weeks old, grown in the dark: 19. No. DAOM 31251. 20. No. DAOM 31252.

sionally forked, $2.1\text{--}2.8\ \mu$ diameter. *Submerged mycelium*: hyphae as in the aerial mycelium, $1.1\text{--}4.9\ \mu$ diameter.

TYPE OF ROT: White.

INTERFERTILITY STUDIES

The two cultures from Cinema and Quesnel, British Columbia, Nos. DAOM 31251 and DAOM 31252, when inoculated on malt agar in Petri dishes and kept in the dark at room temperature for seven and nine weeks respectively, fruited and shed spores. As the two cultures were known to have clamp connections, it was decided, by isolating single spores and pairing the cultures derived from them, to find out if *Aporpium caryae* is homothallic or heterothallic, and, if heterothallic, whether it has the bipolar or tetrapolar type of interfertility.

Single spore isolations were made from spore deposits obtained from the two fruiting cultures. The single spore cultures thus obtained grew very slowly and it was not until eight to eleven weeks after isolation that they were examined for clamp connections. When examined, the hyphae in the single spore cultures were found to have simple septa only,

		A																	a												
		1	3	5	6	8	10	13	14	17	18	19	22	24	25	2	4	7	9	11	12	15	16	20	21	23					
A	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
	17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
	19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
	22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+					
a	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-					
	4	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-					
	7	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-					
	9	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-					
	11	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-					
	12	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-					
	15	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-					
	16	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-					
	20	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-					
	21	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-					
	23	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-					

FIG. 21. A series of pairings in all possible combinations between single spore isolates from a sporophore of *Aporepium caryae* produced in culture, No. DAOM 31251. The plus sign indicates the presence of clamp connections; the minus sign their absence.

showing that the fungus is heterothallic. Subsequently, two series of pairings were made, each with single spore isolates from one of the fruiting cultures. Twenty-five single spore cultures of No. 31251 were paired together in all possible combinations on slants of malt agar in test tubes. The paired cultures were allowed to grow for six weeks

before being examined for clamp connections. On examination, it was found that the single spore cultures formed two groups according to whether or not they paired with each other, 14 cultures falling into one group and 11 into the other (FIG. 21). Likewise 25 single spore cultures of No. 31252 were paired together in all possible combinations with the same results: two interfertility groups were found to be present, again with 14 cultures in one group and 11 in the other. From these results it is seen that *A. caryae* is heterothallic and has the bipolar type of interfertility.

After the results had been obtained from these two series of pairings, three single spore cultures from each of the two interfertility groups of No. 31251 were paired with three cultures from each of the two groups of No. 31252. These pairings showed complete interfertility, as is usual when pairings are made between single spore isolates from two fruit bodies of the same species obtained from different sources (FIG. 22).

		31251					
		A			B		
		3	6	17	9	20	21
31252	A'	2	+	+	+	+	+
		5	+	+	+	+	+
		10	+	+	+	+	+
		7	+	+	+	+	+
a'		8	+	+	+	+	+
		12	+	+	+	+	+

FIG. 22. A series of pairings between single spore isolates from two sporophores of *Aporpium caryae* produced in culture, Nos. DAOM 31251 and DAOM 31252. The plus sign indicates the presence of clamp connections.

SUMMARY

A description of a sporophore of *Aporpium caryae* (Schw.) Teixeira & Rogers is given with a list of fifteen collections of this species to be found in the Canada Department of Agriculture Mycological Herbarium at Ottawa. Two cultures of the fungus are described and a key pattern number based on those used by M. K. Nobles in her key to the identification of cultures of wood-rotting fungi is given. The results of pairings of single spore isolates from fruit bodies produced by the two cultures show that this fungus is heterothallic and has the bipolar type of interfertility. Single spore isolates from the two fruit bodies were completely interfertile.

ACKNOWLEDGMENTS

The author wishes to express her sincere appreciation to Dr. D. P. Rogers for his interest in these studies and for his kindness in sending her a copy of the paper on *Aporpium* by Mr. A. R. Teixeira and himself previous to its publication.

LITERATURE CITED

1. **Nobles, Mildred K.** Studies in forest pathology VI. Identification of cultures of wood-rotting fungi. Can. J. Research, C, **26**: 281-431. 1948.
2. **Teixeira, A. R. and D. P. Rogers.** *Aporpium*, a polyporoid genus of the Tremellaceae. Mycologia **47**: 408-415. 1955.

DEVELOPMENT OF THE ASCOSTROMA IN PLEOSPORA ARMERIAE OF THE PLE- OSPORA HERBARUM COMPLEX¹

LEWIS E. WEHMEYER

(WITH 27 FIGURES)

The binomial *Pleospora herbarum* (Fr.) Rab. has been used in a very broad sense for a large species complex having 7-septate spores, and a few points of clarification are necessary to fix the position of the isolations used in this study.

In a previous paper (Wehmeyer 1953) the writer stated that all type collections of the basonym *Sphaeria herbarum* examined were not of the genus *Pleospora* and it was proposed that Rabenhorst's type of *Sphaeria allii* be taken as the lectotype of the genus *Pleospora*. Since that time, Dr. D. M. Henderson has thoughtfully sent the writer a slide made from the copy of Fries' type exsiccatus (Scler. Suec. 38) of *Sphaeria herbarum* deposited in the Royal Botanic Garden at Edinburgh. All previous copies of this exsiccatus have shown only a *Phoma*, but his copy bears numerous perithecia of a *Pleospora* with spores which are identical with Rabenhorst's fungus on *Allium*. This material can, therefore, be considered as the lectotype of *Sphaeria herbarum* and of the genus *Pleospora*, and the binomial *Pleospora herbarum* (Fr.) Rab. remains legitimate.

In a previous account (Wehmeyer 1952) it was pointed out that Rabenhorst's exsiccatus of *P. herbarum* (Herb. Myc. II, 547a) has comparatively small, thin-walled perithecia which collapse in a pezizoid fashion with age, and spores measuring $25-34 \times 9-11.5 \mu$. The general conception of the *P. herbarum* perithecia has been that of a large thick-walled sclerotic type.

MATERIALS AND METHODS

The three collections used as a source of isolations for these studies were as follows:

¹ Paper No. 1036 from the Department of Botany of the University of Michigan.

1. *Pleospora armeriae* Cda., on *Lychnis coronaria* Duncan, British Columbia, coll. by Margaret Barr, Apr. 11, 1952. (ascospores $38-50 \times 16-29 \mu$).
2. *Pleospora armeriae* Cda., received from Dr. R. F. Cain as a culture (*Macrosporium*) from leaves of *Arctium*, Nashville, York Co., Ont., Aug. 17, 1952. (ascospores $38-48 \times 16 \mu$).
3. *Pleospora herbarum* (Fr.) Rab., received as a culture from Dr. R. F. Cain, isolated from *Corylus*, Vineland, Ont., summer, 1951. (ascospores $28-35 \times 11-13 \mu$).

The arbitrary spore size alone, selected for the separation of *P. armeriae*, is probably not a natural one, for although collections 1 and 2 fall in this species, collection 3 would fall in *P. herbarum*. In all other respects all three isolations behaved in a very similar manner.

These three isolates were carried on 0.2% maltose-yeast extract agar (MgSO_4 0.6 gms, KH_2PO_4 1.2 gms, maltose 2.0 gms, yeast extract 2 gms, agar 20 gms, H_2O 1 liter). All three produced the rather large, thick-walled sclerotic perithecia which are supposed to be characteristic of *P. herbarum*. On agar, such sclerotia originated in local groups or in a scattered fashion, but seldom developed normally to form ascospores.

Such agar colonies were allowed to develop for 4-5 days until 4-5 cm in diameter and then sterilized wheat stems were laid on the colony. Such wheat stems were soon infected and ascostromata were produced abundantly upon them. Although development was not always entirely normal within such ascostromata, many of them matured ascospores within 45-60 days whether kept at room temperature or placed at 10°C .

Sections of such wheat stems, and blocks from agar cultures, were fixed at various intervals from 4 to 75 days in Sass' (1940) modification (No. II) of Allen-Bouin killing fluid. Most sections were cut at 10μ and stained in either Heidenhain's Haematoxylin or Crystal Violet. The latter proved less satisfactory because of the deep stain taken by the pseudoparaphyses, particularly under poor developmental conditions, which masked other details. All three strains behaved in a very similar manner, although strain 3 produced ascostromata most abundantly and matured ascospores most rapidly (within 45 days) whereas strain 2 was poorest in these respects (ascospores within 75 days).

HISTORICAL

Miyabe (1889), in his study of *Macrosporium parasiticum* Thüm., says that the perithecia arise as a row of short cells which cut off slender branches, which then anastomose to form a parenchymatic plexus of

cells. In the upper center of this plexus there appear refractive cells which begin to elongate and divide. From the tip of these cells there arise one to three branches which grow upward as a palisade and dissolve away the solid parenchyma of the stroma. The asci are said to arise from club-shaped branches of these same cells. It took Miyabe's

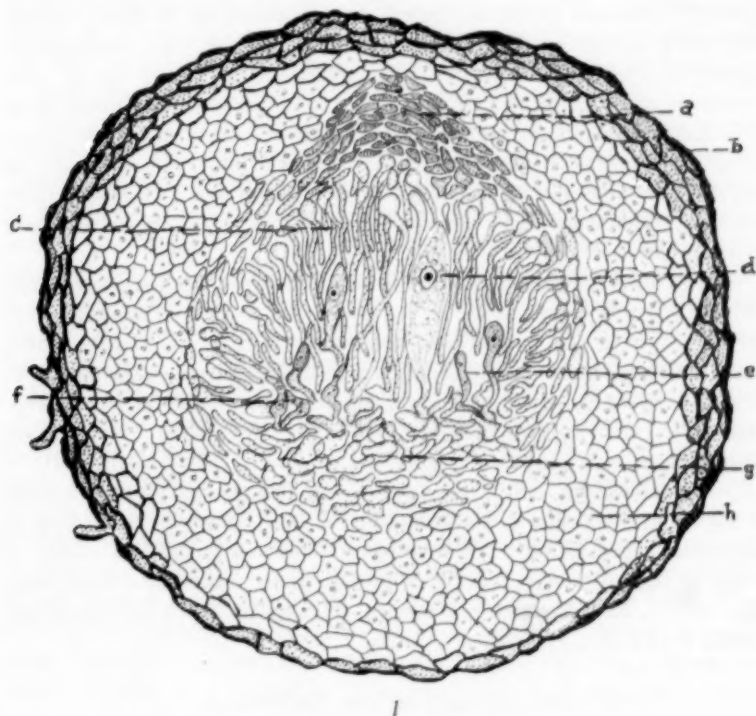


FIG. 1. Diagram of cross-section of young ascostroma of *Pleospora armeriae* Cda. a. apical meristem of dividing cells; b. outer wall of pigmented, thick-walled cells; c. pseudoparaphyses; d. ascus with fusion nucleus just before meiosis; e. young binucleate ascus; f. ascogenous hyphae with crozier-like tips; g. basal area from which ascogenous hyphae and young asci arise; h. hyaline celled parenchyma of ascostroma.

fungus one month to mature ascospores, which were $30-33 \times 12-15 \mu$ and, therefore, would fall in the *P. herbarum* of the writer. This development is similar in general to that found in the present study, but differs in the interpretation of the details.

Cavara and Mollica (1907) gave a much more elaborate interpretation of the development of *P. herbarum*. They state that two gametic cells or hyphae fuse before the formation of the stroma and that the two nuclei of these hyphae also fuse. The ascostroma is then formed by enveloping hyphae, the original "oogonial" cell supposedly dividing to form chains of binucleate cells (although many are uninucleate in their figures). Because of the supposed sinuous character of these chains, their cells appear scattered throughout the ascostroma. Later there appear in this ascostroma refractive sinuous cells which are at first binucleate and then 4-nucleate by mitosis or fusion of cells. From these cells there grow out the palisade of paraphyses, which have uninucleate cells. One cell of such a paraphysis becomes binucleate, increases in size and becomes the young ascus within which the two nuclei fuse. Such a complicated arrangement must be largely imaginative and hypothetical.

Many different conidial fungi have been reported, both by association and by cultural connections, as the imperfect stage of *Pleospora herbarum*. Where the connection was made culturally (Miyabe 1889, Cavara & Mollica 1907, Gibelli & Griffini 1874, Groves & Skolko 1944 etc.) the report has always been of a species of *Stemphylium* (or *Macrosporium*). Groves and Skolko (1944) gave the name *Stemphylium botryosum* to this fungus and gave the conidia as $(14-18-35(-50) \times (12-15-22(-27) \mu$ and the ascospores of the connected *Pleospora* stage as $30-50 \times 15-20 \mu$, which would place it in *P. armeriae* according to the writer's separation. All three of the isolates studied gave rise to ovoid to cubical conidia with dark brown, finely tuberculate walls, usually three transverse and 1-3 vertical or angular septa and measured $18-32 \times 12.5-20 \mu$.

DEVELOPMENT OF THE ASCOSTROMA

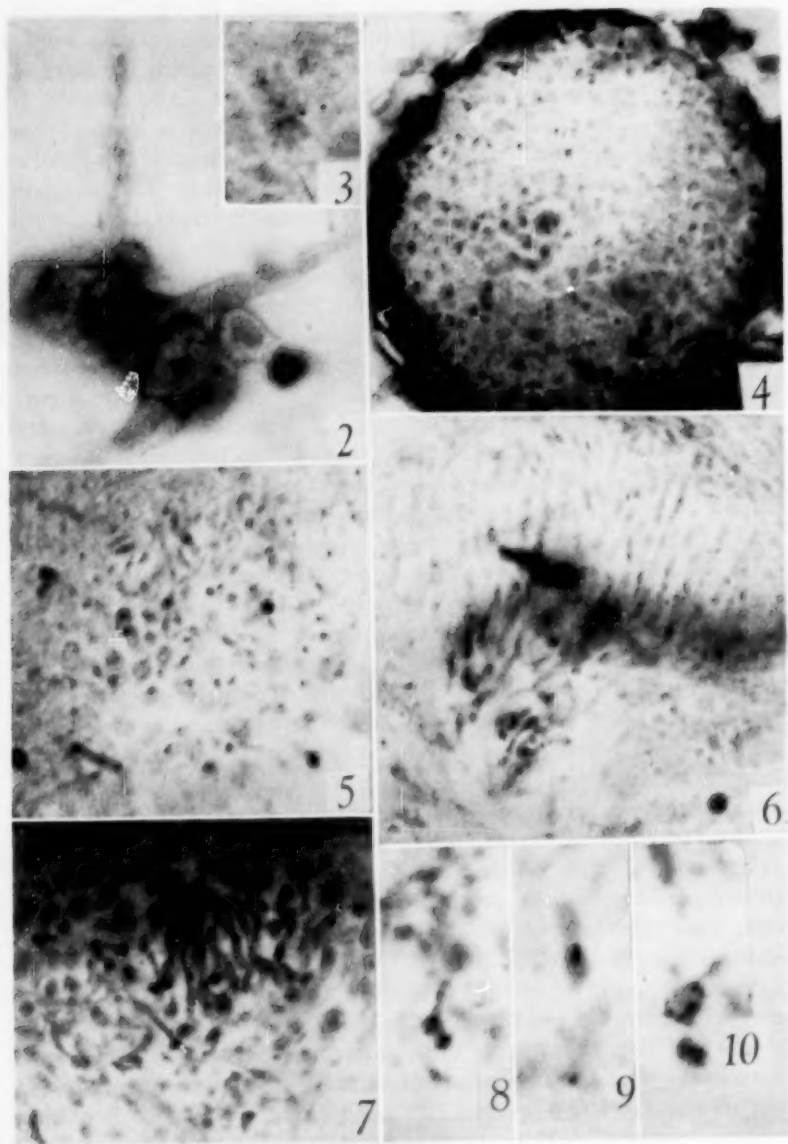
The vegetative hyphae have cells which are uninucleate or binucleate shortly after mitotic division. The nuclei stain faintly and are difficult to make out, but are of the "expanded" type, that is, with a faint network of threads bearing a few minute granules (Fig. 19). Within three or four days after inoculation onto agar or stems, ascostromata are visible to the naked eye. These ascostromata arise as short chains of cells which enlarge and become constricted at the septa (Figs. 2, 19). There may be several adjacent hyphae of this sort. The enlarged cells send out short contorted branches which coil about one another to form a complex knot. The tips of some of these branches grow out as long

tapered hyphae (Figs. 2, 19) which correspond to what have been called trichogynes on the protoperithecia of *Neurospora* etc. No sexual function was observed, however, and these hyphae become the hairs of the young stromata and finally fall off. The larger, more active cells of this knot divide by cleavage to form a mass of hyaline parenchyma of which the enlarging stroma consists. These primordia are similar to the figures given by Miyabe (1889, figs. 8, 9, 17-24). No indication of cell or nuclear fusion was seen at this time, as mentioned by Cavara and Mollica (1907), although it must be admitted that it is almost impossible to follow exactly the nuclear behavior at this point.

Even at this early stage the difference between the progressive and retrogressive course of development mentioned for *Pleospora trichostoma* (Wehmeyer 1954) and *Pseudoplea gaeumannii* (Wehmeyer 1955) can be detected. If conditions are favorable for the development of a particular stroma, the cells retain their granular protoplasm, which takes a deeper stain, and the cells divide rapidly to form a large mass of rather small active cells which are slow to differentiate an outer wall layer. If conditions are not favorable, and the stroma is about to degenerate, it will present a rather small group of larger vacuolate cells which tend to loosen and separate early. The outer cells become thick-walled and pigmented and some of the inner loosened cells will grow out into long filamentous hyphae in a haphazard manner. In either case the cells retain the expanded type of nucleus and are mostly uninucleate.

The first differentiation of well developing stromata comes within the first four to ten days. As the cells divide rapidly and the ascostroma expands there appears a point near the upper center in which the cells become loosened and separated (Fig. 4). This is, apparently, the result of the slowing down of the growth of these cells, which, as space allows, begin to elongate or put out narrow germ-tube-like outgrowths (Figs. 5, 21). Just before or during this differentiation, very small condensed nuclei with a single distinct granule appear in some of the central parenchyma cells, or shortly thereafter in the hyphal outgrowths from these cells (Figs. 3, 20, 21). These can be looked upon as the ascogonia, and the outgrowths from them as the ascogenous hyphae, for they eventually give rise to the asci.

At first, the orientation of these elongating cells or their filamentous outgrowths is in a somewhat indefinite radial fashion (Figs. 4, 5, 21), but shortly a polarity appears (Figs. 5, 6, 7). The cells at the base of this "centrum" remain arranged in an irregular peripheral fashion, but those toward the morphological apex of the ascostroma elongate more or less parallel to one another in a vertical direction forming a

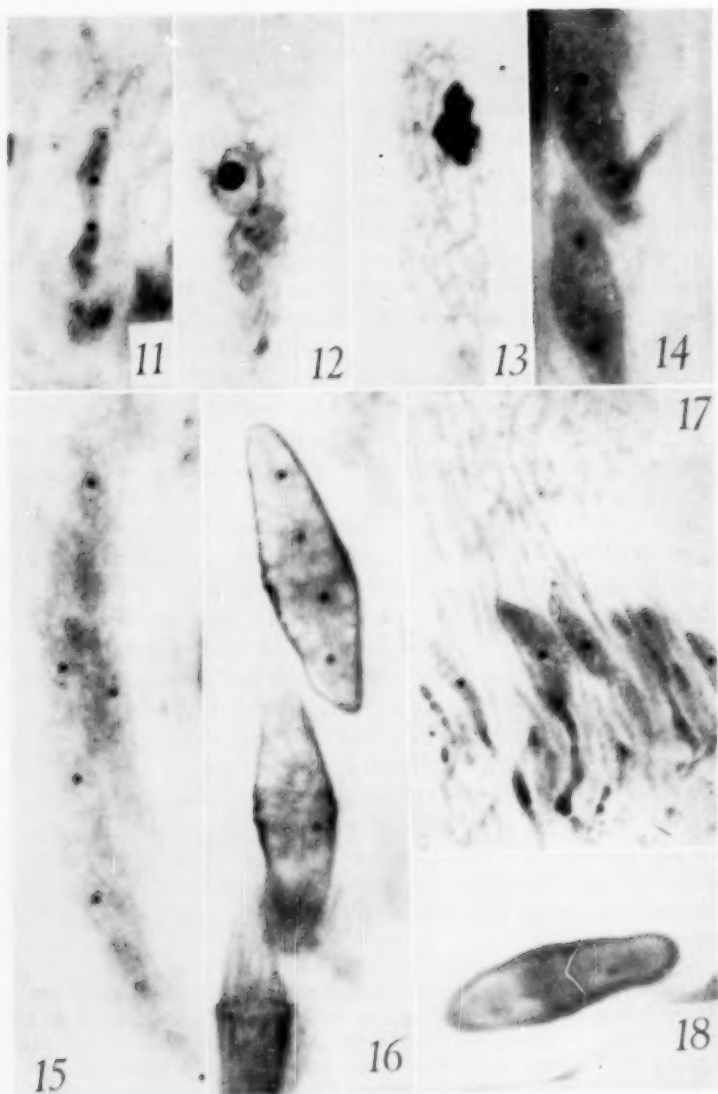


FIGS. 2-10.

palisade of what were earlier called paraphyses, but more recently, by Miller (1949) and Luttrell (1951), have been called pseudoparaphyses (FIG. 1, c). The remainder of the ascostroma continues to expand by the division and increase in size of the cortical cells. Within the centrum this expansion is kept pace with by the elongation of these pseudoparaphyses. These pseudoparaphyses can often be seen attached to cells at the upper margin of the centrum. At the base they merge with the irregular basal layer and their attachment here is difficult to determine, but they seem to have free ends in many cases at least. It is next to impossible to follow single hyphae from the top to the bottom of the centrum, but they can probably be attached at either end and increase in length by elongation rather than any concerted downward growth. At the upper margin of the centrum there is formed a small meristematic area where the cells remain small, actively dividing and deeply staining (FIG. 1, a). Although this area results in the formation of little or no protrusion of the stroma, it serves as a weakened area for the rupture of the stroma and expulsion of the asci.

In the earlier stages of the differentiation just mentioned there appear certain cells which take a somewhat deeper stain and in which the nuclei appear in the condensed form as a single globose granule. Such nuclei are at first $0.2-0.5\ \mu$ in diameter but continue to enlarge from this point onward. They may first be seen in parenchyma cells (FIGS. 3, 20) which can be considered the ascogonial cells, or in the outgrowths from such cells (FIG. 21), which are then the ascogenous hyphae. In the early stages of centrum differentiation such ascogenous hyphae may be found in the upper pseudoparaphysis area, when they usually cut across their vertical orientation, but subsequently they arise from the basal area of unoriented cells (FIG. 6). Very shortly after their appearance these enlarging nuclei appear in pairs (FIGS. 6, 22). No evidence was seen of the fusion of cells or transfer of nuclei, although such behavior would be difficult to determine. The pairs seem to be the result of mitosis.

FIGS. 2-10. 2. Primordium of ascostroma with "trichogyne-like" branches. 3. Multinucleate cell from young centrum showing early appearance of condensed type of nuclei. 4. Young ascostroma, showing the beginnings of separation of the cells of the centrum. 5. Somewhat later stage of centrum differentiation, showing loosening of cells and beginning of elongation of pseudoparaphyses above. 6. Later stage of centrum development, showing a group of ascogenous hyphae with condensed nuclei below the developing pseudoparaphyses. 7. Intermediate stage of centrum showing early development of pseudoparaphyses. 8, 10. Enlarged apex of ascogenous hyphae, from which the young ascus grows out. Each binucleate in these examples. 9. Ascus figure which suggests nuclear fusion.



FIGS. 11-18.

FIGS. 11-18. 11. Binucleate ascus. 12. Fusion nucleus just before meiosis with distinct nuclear membrane and large nucleolus. 13. Beginning of meiosis? Nuclear membrane collapsed about the nucleolus (see Fig. 23). 14. Binucleate

The remaining cells of the centrum (and those of the stromatal cortex) retain nuclei of the expanded form which are difficult to differentiate. Those in the upper part of the centrum continue to elongate to form the palisade of pseudoparaphyses (Figs. 6, 17), which in active stromata are 1–1.5 μ in diameter and with a very thin wall, if any. In stromata, under unfavorable conditions, these pseudoparaphysis strips become broader, crowded and form a wall which takes a deep stain with crystal violet.

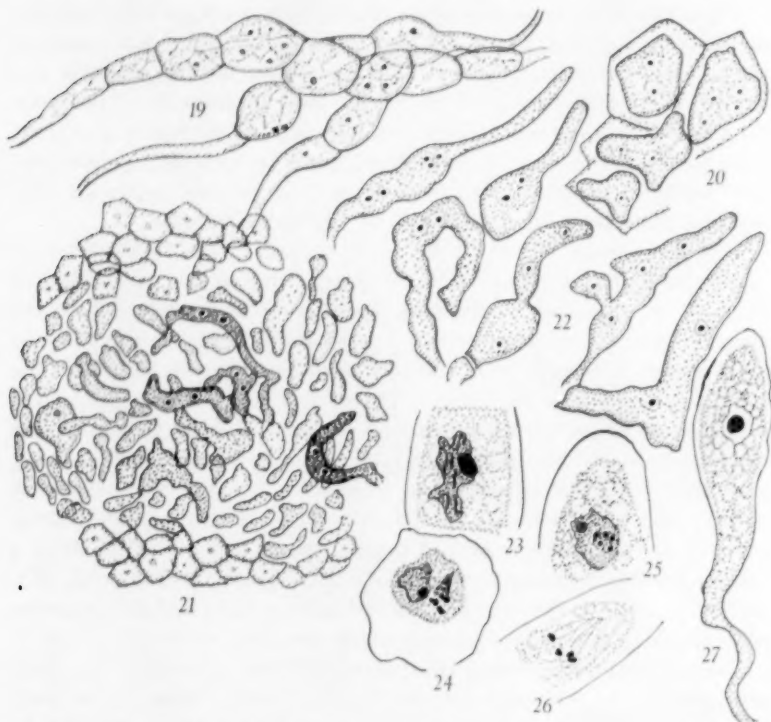
The ascogenous hyphae continue to originate as outgrowths from the unoriented ascogonial cells at the base of the centrum and grow upward between the pseudoparaphyses. Their apices are usually clavately expanded or curved (Figs. 1, a, 8, 10, 22) and simulate the appearance of ascus croziers, but the nuclear configuration is not that of a crozier. There are usually two, sometimes three, nuclei in such an expanded tip. The young ascus grows out from it as a somewhat expanded filamentous projection, into which two of the nuclei migrate.

The two nuclei in the young ascus (Figs. 1, e, 11) continue to enlarge until they are 1–1.1 μ in diameter. Only a few vague figures (Fig. 9) of these two nuclei close together or apparently within the same membrane have been seen, to suggest fusion. However, fusion no doubt occurs, for shortly after this stage a single larger nucleus, 1.2–1.6 μ in diameter, is seen in the ascus. There seems to be a long rest period after nuclear fusion during which both the ascus and the fusion nucleus enlarge greatly. The young ascus is filled with a dense, deeply staining protoplast, but as it enlarges and pushes up between the palisade it becomes highly vacuolate (Figs. 13, 27.) The nuclear granule reaches a size of 2–2.5 μ in diameter just before meiosis and is seen to lie in a definite nuclear membrane some 3–4.5 μ in diameter (Figs. 12, 27). Just before meiosis the enlarging ascus begins to form a thick gelatinous wall, which appears as a clear area about the apex of the protoplasm.

Meiosis and the following third division in the ascus must take place very rapidly, for although thousands of asci with fusion nuclei were seen, only a few vaguely distinct figures were seen which could be referred to meiosis. Fig. 12 shows the appearance of the nucleus just before meiosis. Figs. 13 and 23 are a photograph and drawing respectively of a situation often seen which appears to be the beginning of meiosis. The nuclear membrane takes a deeper stain and collapses

spore primordia. 15. Sixteen-nucleate ascus. Note smaller nuclei, which are at same magnification as in Fig. 14. 16. Two-celled, four-nucleate spores. 17. Young ascostroma centrum with asci with fusion nuclei growing up between the pseudoparaphyses. 18. Four-celled spore with two nuclei in each cell.

about the nucleolar granule. FIG. 24 shows a cross section of an ascus in which the nuclear membrane has broken down and the nuclear granule seems to have broken up into several lumps. FIG. 25 is a similar figure in vertical section showing five granules and what appears to be a disintegrating nucleolus. FIG. 26 shows an ascus with a group of such granules and what appears to be the formation of a spindle. These were the only probable figures of meiosis seen.



FIGS. 19-27. 19. Origin of ascostroma primordium from a vegetative hypha, with expanded nuclei. 20. Parenchyma cells from very young centrum showing origin of condensed type of nuclei. 21. Early differentiation of the centrum, showing separation and elongation of the cells and origin of the ascogenous hyphae with enlarging nuclei of the condensed type. 22. Six apical portions of ascogenous hyphae showing the crozier-like configuration and outgrowth of the young ascus. 23. Early stage of meiosis (as shown in FIG. 13) showing collapse of nuclear membrane. 24. Stage in meiosis showing collapsed membrane and what appears to be fragmentation of the nucleolus. 25. Similar stage with apparently five granules and a disintegrating nucleolus. 26. Meiotic figure suggesting spindle formation. 27. Ascus with fusion nucleus just before meiosis.

Neither were any 2-, 4-, or 8-nucleate asci seen. FIG. 15 shows one focal plane of a 16-nucleate ascus. Spore primordia are scarcely visible here, and such primordia are apparently binucleate at the time they are cut out, as seen in FIG. 14. The nuclei are reduced in size during these divisions in the ascus. They are smaller in the early 16-nucleate condition than in the binucleate spore primordia, so that there must be a period of nuclear enlargement in the spore (see FIGS. 14 and 15). While still in the binucleate condition the spore primordium begins the thickening and pigmentation of its wall. There follows a division of the protoplast and the formation of a central septum, followed by a mitotic division of the nucleus isolated in each cell, resulting in a two-celled, 4-nucleate spore (FIG. 16). This is followed by the formation of a septum between each of the two nuclei of each of the two cells of the two-celled spore. There follows a mitosis giving two nuclei in each of the resulting four cells. Such nuclei in such a spore can be faintly seen in FIG. 18. By this time the spore wall has become so thick and deeply colored that no nuclear detail can be seen within. However, there follows the formation of vertical walls in each of the four cells, which probably isolates the two nuclei seen in such cells. There follows the formation of transverse walls in all of the four cells of such a spore, giving rise to the mature 7-septate spore. The chronologic details of spore formation in the various species of *Pleospora* are of interest because of the diagnostic value of spore septation and morphology. The formation of vertical walls in the four cells of a 3-septate spore, for instance, is what results in the condition previously referred to as *vulgaris*-type septation. Up to and beyond the 3-septate stage the spore is increasing in size and has a pliant cell wall, which obviously accounts for a great deal of the variation in spore form which results from crowding in the ascus.

DISCUSSION

The character of the centrum and particularly the method of development of the paraphyses, paraphysoids or pseudoparaphyses have been used in recent years for the separation of such orders as the Sphaeriales, Hypocreales, Dothideales, Pseudosphaeriales and has been carried over into other orders such as the Hemisphaeriales for the segregation of various taxa. Inasmuch as the terms sphaeriaceous, pseudosphaeriaceous, dothideaceous, etc., have been used as vague generalities without a clear-cut distinction as to their meaning, and have been used by different investigators in quite distinct ways, and inasmuch as various intermediate types have been reported and no doubt exist, it is particularly important to understand the finer details of such development.

Von Höhnelt (1907) in his original discussion of the Pseudosphaeria-ceae believed that the interthelial strips were formed by the crowding of the original parenchyma cells of the ascostroma by the developing asci into filiform "pseudoparaphyses" and stated that they differed from true paraphyses in their resulting attachment at both top and bottom to the parenchyma cells of the stroma surrounding the centrum. Theissen and Sydow (1915) separated the Dothideales and the Pseudosphaeriales merely upon the basis of the number of locules in the stroma, one in the latter and more than one in the former. Miller (1949) limited the Dothideales to those forms, whether with one or several locules, which had no pseudoparaphyses in his sense, but whose asci merely lay free in cavities within a stroma. It will be well to quote his remarks upon the Pseudosphaeriales, which were as follows: "Previously the writer has thought that the threads (see fig. 22) in the centrum attached at top and bottom were remnants of stromal tissue in process of dissolution by developing asci. Since then thin sections of young stages of many species have shown the presence of these threads before the asci even begin to form. The archicarp develops first in the stroma, followed by a fan-like downward growth of threads from the position of the archicarp. Then as the stroma develops the threads elongate and the asci arise at their bases. The connection between these vertical threads and the asci has never been satisfactorily explained. Sartoris and Kauffman (23) and Cavara and Mollica (3) thought the young asci were formed in the threads. Dodge (5) with *Leptosphaeria* and Wehmeyer (31) with *Pseudotrichia* thought there was no connection with the asci." Miller furthermore supposed that a similar type of development, but within a true perithecium with a typical perithecial wall, should characterize the Hypocreales. Luttrell (1951) follows Miller's suggestions. *P. herbarum* is typical of Luttrell's *Pleospora* type within the Pseudosphaeriales. Concerning the interthelial tissue he states, "In the region of the stroma occupied by the ascogonia a group of vertically arranged separate hyphae appears. These hyphae are the pseudoparaphyses (paraphysoids, interthelial threads). The pressure exerted by the elongation of the pseudoparaphyses creates the flask-shaped locule of the stroma. The pseudoparaphyses are attached at both the top and bottom of the locule and, consequently, may be distinguished from paraphyses." These variations in opinion, which lead to the difficulties of applying them to a general classification, both stem from the fact that the details of the development of the centrum are not known in the great majority of species and that as they become known, many different types and gradations in this development will no doubt appear.

In the case of *P. armeriae*, the writer's observations agree in general with those of Miller and Luttrell, but vary in certain details and interpretations. The pseudoparaphyses can hardly be said to "grow down from the top," nor does the pressure of their growth form the locule, for they are too loosely arranged. Rather, the entire ascostroma enlarges as a unit. The cortical cells outside the centrum, which region is often referred to as the wall, are compacted, angular and adjacent but increase in size and, toward the center, continue to divide. In the centrum region, this type of division and enlargement is in abeyance and the cells here become separated. As soon as there is free space they begin to elongate or push out short projections as described. Beyond this point, the elongation of the pseudoparaphyses and the proliferation of the ascogenous system in the base of the centrum merely keep pace with the growth of the stroma as a whole. There is, to be sure, a sort of downgrowth, because the pseudoparaphyses arise for the most part from cells in the upper portion of the centrum. They do not appear to be attached at both ends. Free ends are commonly seen, usually at the base of the centrum. They probably can also extend upward from the base, but these basal cells usually give rise to ascogenous hyphae.

The structures referred to as archicarps or ascogonia by various writers no doubt correspond to the differentiating cells in which the nuclei of the condensed type appear, often in pairs, and the outgrowths from these cells correspond to the ascogenous hyphae. Sartoris and Kauffman (1925) picture a type of development in *Apiosporina* in which the penultimate cell of a crozier gives rise to the young ascus and the ultimate cell grows out as a pseudoparaphysis, and Cavara & Mollica (1907) suggest that the ascus arises from a binucleate cell in the pseudoparaphysis in *Pleospora*. Arnold (1928) cites downward growing paraphyses in *Sporormia* and states that the terminal cells of these filaments enlarge and give rise to the young asci which turn upward and grow between the palisade. In sections where a young ascus exactly overlies a pseudoparaphysis filament it often appears a part of the pseudoparaphysis itself, but careful focussing usually resolves it as distinct. In *P. armeriae*, at least, the young asci always arise at the apex of upward growing ascogenous branches arising from the basal cells. In *Pleospora trichostoma* (Wehmeyer 1954) the differentiation of ascogenous hyphae and pseudoparaphyses is not so distinct and in *Pseudoplea gaeumannii* the interthecial tissue is composed of the actual compressed parenchyma cells of the stroma as described by Höhnelt.

Such variations and differences of opinion suggest caution in the use of these characters as major distinctions in a general classification

until the detailed development of many more species is known for comparison.

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SOME LEAFSPOT FUNGI ON WESTERN GRAMINEAE. IX¹

RODERICK SPRAGUE

(WITH 1 FIGURE)

This paper continues the series of articles on the parasitic leafspot fungi on the grass family in western North America. The two previous articles dealt with collections made in Alaska in 1952 (15, 16). The present paper discusses fungi collected in the mountains and fields of north central Washington or nearby Idaho and some material that had been obtained earlier in the Rocky Mountain region on travels with G. W. Fischer (cfr. 11, 12, 13). One specimen was also furnished by W. B. Yerkes from a collection made by M. Zenteno in Mexico. There are also herbarium fragments from some phanerogamic sheets from the far north. A number of specimens were also obtained by the writer and Mary Willis Sprague in Glacier National Park, Montana, August 27, 1954, some of which are herein noted.

Hyalothyridium sorghicola sp. nov.

Pycnidii paucis, sub-gregariis, immersis, globosis, ostiolatis, brunneis, 125-170 μ ; pycnosporulis hyalinis, muriformibus, transverse 3-4-septatis, 1-2-septatis longitudinaliter, cylindraccis v. ellipsoideis, vel obovatis, ad septa constrictis, apicibus et basibus rotundatis, 22-25 \times 11.5-13.0 μ .

Socia Helminthosporii turcici et Phyllostictae sorghinae in maculis Sorgho vulgari Pers.

Pycnidia few, somewhat gregarious, immersed, finally erumpent, obscure, globose, ostiolate, brown, 125-170 μ diam.; pycnospores hyaline, muriform with 3-4 cross walls and 1-2 longitudinal cell walls, the latter usually in the next-to-basal cell or sometimes the third or fourth cell from the base, cylindrical but deeply constricted at the cross walls in older spores, hence irregular, somewhat the shape of a mulberry fruit, sometimes obovate and usually approaching an ellipsoidal shape because of the round but smaller end cells, contents hyaline or only lightly tinted, 22-25 \times 11.5-13.0 μ .

¹ Scientific Paper No. 1381, Washington Agricultural Experiment Stations, Pullman. Project No. 449.

In spots associated with *Helminthosporium turcicum*, *Phyllosticta sorghina* and various molds. Pycnidia, which were few, are preserved on a dry glass slide. Probably nonparasitic but found on living leaves of *Sorghum vulgare* Pers., Chapingo, Mex. Coll. M. Zenteno, August 4, 1952. Type specimen fragment removed from Herb. Crit. Off. de Estudios Especiale S.A.G. 1179 and filed as WSP 33,576,² Pullman, Washington. Bulk of packet returned to Mexico City, D.F.

This was compared with Greene's description of *H. calamagrostidis* (5) which has larger spores ($30-45 \times 16-23 \mu$).

ASCOCHYTA SORGHI Sacc. is associated with *Hendersonia crastophila* Sacc. on *Festuca elatior* collected at Worland, Wyo., June 26, 1946, but the spores of the former were nonseptate (*Phyllosticta*) when examined in 1946. The temporary water mount was ringed with vaseline and laid aside. It was not re-examined until 1951. Apparently the water had been retained long enough to permit germination of the *Hendersonia* spores and for septations to form in the previously nonseptate *Ascochyta* spores. They were $11-16 \times 2.3-2.7 \mu$ and could be assigned to *A. sorghi*. This therefore deletes the "*Phyllosticta* sp." from the records and adds *A. sorghi* on a new host. Grove (6) described *A. graminicola* var. *festucae* on *F. ovina* with fusoid spores $14-17 \times 3 \mu$. Our material is different in the fact that the spores are cylindrical or only faintly fusoid. The Wyoming collection is fairly typical of summer material of *A. sorghi*.³

PHLESPORA MUHLENBERGIAE Sprague and Solheim in Solheim was found on *Muhlenbergia filiformis* (Thurb.) Rydb. in an alkali flat seven

² These are accession numbers for the Mycological Herbarium, Department of Plant Pathology, State College of Washington. Since specimens filed in this herbarium are separately accessioned, the abbreviation WSP is used to distinguish them from those filed in the Herbarium, State College of Washington (WS. See Lanjouw and Stafleu, 1954. The herbaria of the world. Regnum Vegetabile 2. ed. 2. 179 pp.).

³ A specimen of *Phyllosticta* on *Muhlenbergia schreberi* Gmel. was collected along the street on upper Harvard Avenue, Cambridge, Mass., on August 31, 1952, by myself (WSP 33,607). While outside the geographical range of this paper, it is appended here as comparable material to that above-mentioned. The spores were irregularly cylindrical or flattened on one side and the contents contain a number of oil drops (Fig. 1C). The spores tend to cling together and are obviously immature. They measure $9-13 \times 3.2-4.1 \mu$. I believe that these are immature, heat-inhibited, summer spores of *Ascochyta sorghi* Sacc. The pycnidia are abundant on yellow-brown leaves of the current season and appear to represent parasitic activity. The spores are slightly wide for *A. sorghi* but the evident parasitic nature and the abundant production of pycnidia indicate *A. sorghi* rather than *A. brachypodii*. This appears to be an addition to the Massachusetts fungus flora.

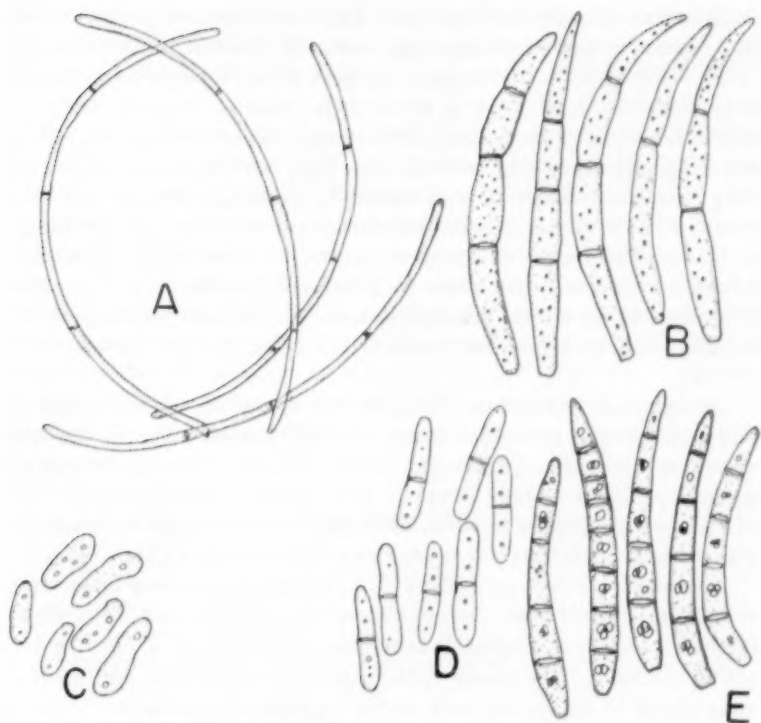


FIG. 1A. Pycnospores of *Septoria tandilensis* Speg. from the type of *Phleospora panici* H. C. Greene. B. Pycnospores of *Phleospora muhlenbergiae* on *Muhlenbergia filiformis*, Lakeside, Montana (WSP 24,318). C. *Phyllosticta* phase of *Ascochyta sorghi* Sacc. on *Muhlenbergia schreberi*, Cambridge, Mass. (WSP 33,607). D. *Ascochyta* phase of *Septoria nodorum* on *Melica smithii*, Sprague Creek Camp, Glacier National Park (WSP 33,229). E. Pycnospores of *Stagonospora intermixta* on *Agrostis palustris*, English Camp, San Juan Is. (WSP 24,317).

All drawings made with the aid of a camera lucida and reproduced at a magnification of approximately $\times 1000$.

miles east of Lakeside, Montana, August 11, 1950 (WSP 24,318). The spores are the same as in the type (8, p. 628) except that they are longer, $37-55 \times 3.5-4.4 \mu$ as compared with $21-45 \times 2.6-4.0 \mu$. A few are 3-septate while the type has 1- to 2-septate spores. The spores in the type are chlorine-yellow with homogeneous contents and those in the Montana collection have very small globules in the protoplasm (Fig. 1B). This fragment extends the host range and also the geographical range, the only other report being the type on *M. arizonica* from Arizona.

SEPTORIA OUDEMANSII Sacc. was found on leaves of *Setaria viridis* (L.) Beauv. in an orchard near Leavenworth, Washington, October 10, 1952 (WSP 24,389). The spores are typical for *S. oudemansii*, lanceolate-cylindrical, slightly larger in the center than at the ends, 1-septate, with small oil-drop inclusions. The spores measure $15-21 \times 2.1-3.5 \mu$ and are produced in long tendrils from light brown pycnidia about 70-100 μ diameter. Since *S. oudemansii* is almost omnipresent on *Poa pratensis* in the region it is believed conservative to consider the fungus on this unrelated grass as the same fungus. *Setaria* is seldom listed as a host for *Septoria* and when so listed the species is usually called *S. graminum*, an utterly different species with filiform spores. *Setaria* is unreported as a host for *Septoria* from the western United States (cf. 14).

ASCOCHYTA UTAHENSIS Sprague was found on mottled areas on leaves of *Elymus triticoides* Buckl. at 8500 feet elevation in dry pine woods on Pike's Peak, Colorado (WSP 24323). The spores had the single septation acentrally located. The spores measured $25-30 \times 9.8-11.2 \mu$ and were similar to other *Apiocarpella*-like material of this fungus which was reported several years ago on *Agropyron* (12, p. 558).

SEPTORIA INFUSCANS (Ell. & Ev.) Sprague was found on a previously unreported host, *Agropyron inerme* (Scribn. and Sm.) Rydb., three miles north of Chelan, Washington, following heavy rains in 1953 (WSP 33,528). The coarse spores and large pycnidia in dark blotches were typical of the malady as it occurs on *Elymus condensatus* Presl, its most prevalent infected host in the West.

STAGONOSPORA INTERMIXTA (Cooke) Sacc. has been reported from Wisconsin on *Agrostis alba* L. (2, 3, 4). Davis first noted it (2) with 7-septate spores $43-48 \times 3.5 \mu$. Later he deleted this host because of the scanty material (3) but Greene (4) found it again on *A. alba* in the state. Greene reported shorter spores, $30-40 \times 3 \mu$, but they too were 7-septate. Davis had earlier reported atypical material (1) on *Cinna arundinacea* with 7-septate spores $40-60 \times 3.5-5.0 \mu$. In a recent general manual we included *St. intermixta* as a somewhat vague, unsatisfactory species having 7 septations instead of 3 septations (14).

We now have material on *Agrostis palustris* Huds. collected at English Camp, San Juan Island, Washington, on August 15, 1950 (WSP 24,317) that we are placing in *St. intermixta* for want of a better place. The spores are stiffly curved, often bent at the basal septum, abruptly pointed at the apex but blunted at the base (FIG. 1E), 3- to 4-, but sometimes 5- or 7-septate. The contents are coarse, faintly yellow and measure $25-40 \times 3.5-4.3 \mu$. This fungus does not belong

in *Septoria avenae*, which has clear, hyaline, uniformly 3-septate spores. The San Juan collection has spores with the shape of *St. agrostidis* but this species and *St. insularis* Speg. have somewhat shorter spores, which also are 3-septate. We could place our material in *St. arenaria* Sacc. if we followed Grove (6) who reported the type had 3- to 5- (or even 6- to 7-) septate spores. We have hesitated to accept this statement since the type description mentions no spores with more than 3 septa. Such material as the type of *St. arenaria* on culms often involves several fungi and Grove could have seen an associated species not noted by Saccardo. The material from English Camp resembles some 3-septate material on *Dactylis* from Wallace Bridge, Oregon, which we placed in *St. arenaria* (14, p. 272, Fig. 55d) but is smaller than some Washington material of *St. arenaria* on *Dactylis* (14, p. 221, Fig. 27f). Without the type of either *St. intermixta* or of *St. arenaria* we are forced to rely on available information and place our collection, as mentioned, in *St. intermixta*.

OVULARIA PUSILLA (Ung.) Sacc. & D. Sacc. **emended**

- Ramularia pusilla* Ung. 1833
- ?*Cacoma pusillum* Bonord. 1860
- Ramularia pulchella* Cesati 1853
- Ovularia pulchella* (Ces.) Sacc. 1886
- Ovularia pulchella* var. *lolii-italici* Ferr.
- Ovularia pulchella* var. *agropyri* Davis 1919
- Ophiocladium hordei* Cav. 1893
- Ovularia hordei* (Cav.) Sprague 1946
- Ovularia baldingeriae* Eliasson 1915
- Ovularia holci-lanati* Cav. 1893
- Ramulaspora holci-lanati* (Cav.) Lindau 1907
- Ovularia lolii* Volkart 1903

Young lesions round to elliptical, 1-5 mm diameter, on some hosts lesions become elongate to striate, sometimes $10-30 \times 1-5$ mm, brown or tan with red borders, later ashy or straw color, or without borders or surrounded by a diffuse buff area (on *Phalaris*) but typically a small eyespot; amphigenous. Conidiophores in compact hyaline fascicles in neat rows between the veins of the leaf, emerging from stomata and arising from abundant yellow to mostly hyaline compacted mycelium, the conidiophores serpentine or straight, $20-65(-170) \times 2-4(-4.5) \mu$; conidia acropleurogenous, on breaking off leaving a slight hilum at the base of the elliptical to elongate-ovate hyaline spores, non-septate, sometimes with an evident wall which is faintly roughened to distinctly muriculate; at other times, in younger spores, smooth and with no very apparent double spore wall $(7-)8-17(-27) \times 6-13 \mu$.

On: *Agropyron cristatum* (L.) Gaertn., Colo.; *A. repens* (L.) Beauv., Ont.; *A. subsecundum* (Lk.) Hitchc., Mont.; *A. trachycaulum* (Lk.) Malte, Wisc.; *Agrostis acquivallis* (Trin.) Trin., Alaska; *A. alba* L., Oregon, Utah, Wash., Wisc.; *A. exarata* Trin., Alaska; *A. humilis* Vasey, Wyo.; *A. oregonensis* Vasey, Mont.; *A. palustris* Huds., Oregon; *A. tenuis* Sibth., Utah; *Alopecurus alpinus* J. E. Smith, Mont.; *Arctagrostis latifolia* (R. Br.) Griseb., Alaska; *Arrhenatherum elatius* (L.) Beauv., Oregon; *Bromus carinatus* (Hook.) Arn., Ida., Wash.; *B. inermis* Leyss., Ida., Wash., Wisc.; *Calamagrostis canadensis* (Mich.) Beauv., Mont.; *Deschampsia atropurpurea* (Wahl) Scheele, Alaska; *Elymus glaucus* Buckl., B.C., Mont., Wash.; *Festuca idahoensis* Elmer, Ida.; *F. kingii* (S. Wats.) Cassidy, Colo., Utah; *F. megalura* Nutt., Oregon; *F. myuros* L., Oregon; *F. rubra* L., Alaska; *Glyceria elata* (Nash) Hitchc., Wash.; *G. erecta* Hitchc., Calif.; *G. grandis* S. Wats., Wisc.; *G. pauciflora* Presl, Alaska; *Holcus lanatus* L., Oregon, Italy; *Hordeum brachyantherum* Nevski, Alaska; *Lolium marschallii* Stev., Oregon; *L. spp.*, Argentina, Europe; *L. multiflorum* Lam., B.C.; *L. perenne* L., B.C., Oregon; *Melica bulbosa* Geyer, Mont.; *Phalaris arundinacea* L., Ida., Mont., N. Dak., Wisc., Wyo.; *Poa ampla* Merr., Ida., Wyo.; *P. laxiflora* Buckl., Alaska; *P. longiligula* Scribn. & Wils., Wyo.; *P. pratensis* L., Alaska; *Trisetum spicatum* (L.) Richt., Wyo.

In keeping with modern trends it now seems necessary to group all of the *Ovularia* spp. on Gramineae in one species. We have endeavored in earlier papers (9, 10, 11, 12, 13, 14) to follow tradition and recognize two well-known phases of this species. Certain mature specimens with stout to elongate conidiophores bearing somewhat spiny spores with evident walls we have called *O. hordei* (9, 10, pp. 309-10). Those with smooth to faintly spiny spores were placed in *O. pusilla* (9, 10, pp. 309-10). With the increase in known host range and with abundant material now available it is clear to us now that segregation along the lines employed earlier is no longer practical. Some material found earlier on *Festuca kingii*, for instance, has the characters of both species (10). Still more recently we have examined leafspot material on *Agropyron subsecundum* (Lk.) Hitchc. which has definitely spiny spores in part of the material (WSP 24,307) and stout conidiophores in another collection (WSP 24,322) bearing spores referable to either species. These collections were obtained August 11, 1950, near Sheep Mountain on the shores of Upper Red Rock Lake in southern Beaverhead, Montana. This material, coupled with many other collections made during the past 24 years, convinces me that too many intermediate collections now occur to warrant keeping the two species segregated.

While *O. pusilla* is seldom of any great economic importance, on June 29, 1953, we encountered a field of smooth brome (*Bromus inermis* Leyss) near Winthrop, Washington, that was heavily spotted (WSP 33,634). There were as many as 140 lesions on an individual leaf. The small round spots were ashy brown with yellow borders, typical for the fungus on this host-genus. The spores were $10-14 \times 6.8-7.6 \mu$, definitely asperulate, typical in shape for the species. Almost 100 percent of the leaves on the lower half of the heading plants were spotted and many were chlorotic and dying from the infection. The fungus was also common on *Elymus glaucus* Buckl. in the vicinity (WSP 37,281) in 1954.

CURVULARIA GENICULATA (Tracy & Earle) Boed. was common on dead leaves of living plants of *Digitaria ischaemum* (Schreb.) Muhl. near Leavenworth, Washington, October 24, 1951 (WSP 24,335). The spores were typical of those illustrated previously (14, Fig. 71) measuring $25-30 \times 10-15 \mu$. This fungus is a common saprophyte on many hosts. It is only mentioned here because this material seems to represent mild parasitism on this somewhat exotic host.

RHYNCHOSPORIUM SECALIS (Oud.) J. J. Davis was common on *Agropyron intermedium* (Host.) Beauv. in the Geaudreau meadows near Blanchard, Idaho, on June 13, 1953. The meadow had been seeded to a mixture of alfalfa and the wheatgrass the year previous. Infection had probably come from *A. repens*, which was heavily infected in the general area. The intermediate wheatgrass appeared to be less susceptible than quack grass. *A. intermedium* is an unreported host.

FUSARIUM NIVALE (Fr.) Ces. formed obscure small pink mounds of spores on elongate buff lesions on *Agropyron cristatum* (L.) Gaertn. collected by K. W. Kreitlow at the Northern Great Plains Field Station, Mandan, North Dakota, on June 23, 1953 (WSP 33,656). The spores were 0- to 1-septate, $9-14 \times 1.8-3.0 \mu$, borne on branched conidiophores. The presence of this snow mold on living leaves of a grass in late June is unusual. Leaf spotting due to *F. nivale* is widespread in early spring in eastern Washington following wet snows or cold driving rains but is seldom noted on living leaves after April and May. It can, however, be isolated from the roots of plants until late spring. It is, in fact, far more common in the West than is generally recognized. In some work with snow mold of winter wheat near Mansfield in Douglas County, Washington, it was found that even where there was only a trace of *Typhula* spp. fall applications of fungicides resulted in an increase of yield up to as much as 6 bushels per acre. Elimination of the somewhat superficial *F. nivale* was apparently one of the causes for this increase.

The fungus is omnipresent on cereals and grasses during the winter and spring in the region.

ERYSIPHE GRAMINIS DC. was collected on *Poa compressa* L. growing under pines and at the edge of clearings near Blanchard, Idaho, on June 13, 1953, and again on September 19. Infection was relatively heavy. This host is seldom found infected in the Pacific Northwest.

MASTIGOSPORIUM RUBRICOSUM (Dearn. & Barth.) Nannft. occurs on a phanerogamic herbarium specimen of *Calamagrostis nutkaensis* (Presl) Steud. at Thum Bay, Alaska (Walter J. Eyerdon, Plants of Alaska, 3242). The fragment is filed as WSP 37,208. This is a previously unreported host for this leafspot fungus.

SELENOPHOMA DONACIS var. STOMATICOLA (Bauml.) Sprague & A. G. Johnson was found on W. S. C. Herb. sheet 4347 of *Poa suksdorfii* Vasey collected on Mt. Rainier, Washington, at 9000 feet elevation nearly sixty years ago, August 1895, by C. V. Piper (No. 1965). The spores are short, the curved ends not sharp as in *S. everhartii* nor blunt as in *S. obtusa*, $10-13 \times 1.8-2.5 \mu$ in small pycnidia in lines in bleached culms. This is probably in group 4 of var. *stomaticola* (14). This is the first report of a parasitic fungus listed on this little known grass. It appears to be one of the few more or less bunch-grass type of western *Poa* spp. that has survived a recent reshuffling of these collections in the herbarium at W. S. C. *P. suksdorfii* Vasey ex Piper is listed in the revised Hitchcock manual (7) as a synonym of *Poa pringlii* Scribn. Since we also have no fungus listed on *P. pringlii* in the grass disease check list (17), it seems desirable to record this addition here. The specimen is filed under WSP 37,210. Specimen WSP 37,213 collected on the same host by William Cusick in 1909 in the Wallowa Mountains is comparable to WSP 37,210 although the spores are slightly longer.

ERYSIPHE GRAMINIS DC. was found on *Poa arctica* R. Br. collected by the Cornell Party of the Peary Voyage of 1896 (August 12) at Nugssuak Peninsula, Greenland, at about 70° N. Lat. The fragment was noted on a herbarium sheet filed in the Botany Dept. Herbarium, Washington State College. The sheet refers the examiner to Macoun Cat. IV:224. The specimen of Erysiphe is filed as WSP 37,211. Since *P. arctica* is an unreported host and the area collected is so far north, it has been added here although technically considerably removed from "Western."

SEPTORIA TANDILENSIS Speg. was determined on *Panicum multi-rameum* Scribn. collected in a large swamp east of Tactic, Guatemala, Dept. Alta Verapaz, on April 14, 1941, by Paul C. Standley (92,416, Plants of Central America). The typical flattened, black, widely ostio-

late pycnidia are abundant on dead leaves. Most of the pycnidia contain prosenchyma but a few spores, $55-60 \times 1.0 \mu$, were seen. This material was included in some undetermined collections sent by John A. Stevenson from Mycology and Disease Survey collections. The host was determined by J. R. Swallen. The type of *S. tandilensis* was described from Argentina. The fungus is common in Wisconsin. Greene recently sent all of the *Septoria* spp. on *Panicum* from the Herbarium, University of Wisconsin, to the writer and all of the filiform-spored *Septoria* on *Panicum* in their collections were *S. tandilensis*, including *Phleospora panici* Greene. The collection from Guatemala, which closely resembles the type of *Phl. panici*, is interesting in that it indicates that *S. tandilensis* ranges across two continents. *S. tandilensis* also occurs on *Panicum sabulorum* Lam. in Uruguay in the U.S.D.A. collections loaned by Stevenson. It was collected at Florida, Timote, Uruguay by Rosengurtt (B-1635) and determined by E. E. Dicks. The spores in the Uruguay specimen were $50-70 \mu$ long.

Other specimens of *S. tandilensis* noted in the collections sent by Stevenson included: on *P. consanguineum* Kunth., Poplarville, Miss., H. R. Reed, Nov. 23, 1931; on *P. sp.*, upper Sycamore Is., Montgomery Co., Md., E. Cash, U.S.D.A. 70,409; as noted by Cash, spores are $60-100 \mu$ long; *Panicum clandestinum* L., Kingston, W. Va., W. A. Archer, P.D.S. of W. Va. 2096, July 2, 1928; *P. clandestinum*, Potomac Flats, D. C., May 22, 1890, name of collector not given but (his) handwriting is in the packet; on *P. sanguinale*, Newfield, N. J., J. B. Ellis, North American Fungi 750, Sept. 1880; on *P. scribnerianum*, Nebraska (probably Long Pine), Rev. J. M. Bates 3051, Sept. 29, 1903, pycnidia very large. These plus the Wisconsin collections and one by the writer from North Dakota comprise the known collections of this species from the United States. A search of all available collections would no doubt add many more.

FUSARIUM NIVALE (Fr.) Sacc. and *SEPTORIA TENELLA* Cke. & Ellis were noted on *Festuca idahoensis* Elmer at Mary's Lake, Glacier National Park. *SCOLECOTRICHUM GRAMINIS* Fckl. on *Bromus breviaristatus* Buckl. was also collected at Mary's Lake. These are all new hosts for the region.

A 1-septate phase of *SEPTORIA NODORUM* Berk. occurs in brown blotches and leaf tips in a specimen of *Melica smithii* (Porter) Vasey along Sprague Creek, Glacier National Park, August 27, 1954 (WSP 37,229) (FIG. 1D). Microspores of *S. nodorum* were found on *Melica subulata* (Griseb.) Scribn. at the same site (WSP 37,231). Hosts were determined by Dr. Swallen.

COLLETOTRICHUM GRAMINICOLA (Ces.) Wils. was present on *Melica subulata* along Sprague Creek (see above) (WSP 37,230). The spores were $18-22 \times 4 \mu$. The same fungus was seen on *Agrostis alba* associated with *Puccinia coronata* Corda at the same location (WSP 37,235).

SELENOPHOMA DONACIS (Pass.) Sprague and A. G. Johnson was common on *Agropyron subsecundum* var. *andinum* Hitchc. on Logan Pass on August 27, 1954. Conditions were the equivalent of late spring at this elevation. *S. donacis* appears to be almost universal on certain hosts at these high altitudes although this alpine variety of bearded wheatgrass has not been reported as parasitized in the region (WSP 37,233; 37,236; 37,237).

RHYNCHOSPORIUM SECALIS (Oud.) J. J. Davis was noted on *Agropyron repens* at Sprague Creek, Glacier National Park but was uncommon because of the dry season (WSP 37,234).

SCOLECOTRICHUM GRAMINIS Fckl., which was prevalent along the Chewack River near Winthrop, Washington, on June 29, 1953, was noted on *Agrostis scabra* Willd. and *Agrostis exarata* var. *monolepis* (Torr.) Hitchc., both unreported hosts for this fungus in the state of Washington.

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NORTH AMERICAN HYALINE-SPORED SPECIES OF THE GEOGLOSSAEAE¹

E. B. MAINS

(WITH 47 FIGURES)

The Geoglossaceae has been divided by Durand (1908) into two tribes, the Geoglosseae having capitate or more or less compressed-clavate or spatulate ascocarps and the Cudonieae having pileate ascocarps. He included *Microglossum*, *Corynetes*, *Spathularia*, *Mitrula*, *Gloeoglossum*, *Geoglossum* and *Trichoglossum* in the Geoglosseae. The last three genera have brown spores and have been treated in this study in a previous publication (Mains, 1954). The other genera have hyaline spores and are discussed here.

Microglossum as treated here includes *Corynetes*. It is closely related to *Geoglossum*. It has similar compressed clavate ascocarps (FIG. 1). Several species of *Geoglossum* produce both hyaline and brown spores and *Geoglossum alveolatum* only rarely produces brown spores. Although most species of *Microglossum* have much smaller ascospores than those of *Geoglossum*, *M. longisporum* has both long and short spores (FIGS. 16, 17). The ascospores of *Microglossum* are commonly multiguttulate and only rarely septate (FIGS. 16-18, 20, 21, 23). Durand separated *Corynetes* from *Microglossum* on the basis of color of the ascocarps, *Corynetes* having black, brownish black, or purplish black ascocarps and those of *Microglossum* being bright colored (yellow, brown or green).

Spragueola has very irregular ascocarps (FIGS. 5, 6) which in some collections approach the compressed clavate form of *Microglossum*. It differs from *Microglossum* and all other genera of the Geoglossaceae in that it lacks paraphyses and has small ellipsoid ascospores (FIG. 26). Durand included it in *Mitrula*, but it appears to be more closely related to *Microglossum*.

Spathularia appears to occupy an intermediate position between *Microglossum* and *Cudonia* of the Cudonieae. The ascocarps of *Spathularia* are usually more compressed than those of *Microglossum*, being

¹ Paper from the Herbarium and the Department of Botany of the University of Michigan. Published as excess pagination from the funds of the Herbarium.

spathulate with the ascogenous portion extended farther down the stipe on the edges than on the flattened sides (FIG. 7). In *Spathularia flavida* var. *ramosa* there are variants which are compressed-clavate as in *Microglossum* (FIG. 9). The ascospores differ from those of *Microglossum*, being acicular (FIGS. 27, 33, 36, 37, 40), having walls that gelatinize (FIG. 31) and producing conidia on short sterigmata (FIGS. 30, 38). In these characteristics they differ from the other genera of the Geoglosseae and resemble *Cudonia*. The ascocarps of *Cudonia* are pileate with the hymenium on the upper surface of the pileus and with the lower surface sterile, a condition which separates the Cudoniae from the Geoglosseae.

Mitrula has capitate ascocarps with the upper ascogenous portion rather sharply differentiated as a head (FIGS. 10, 12-14). In most species the head is completely covered by the hymenium. However, in *M. abietis* there is a narrow sterile zone between the hymenium and the stipe (FIG. 15) and it appears to occupy an intermediate position between the Geoglosseae and Cudoniae. The ascocarps are small. The fusoid, cymbiform or subcylindric ascospores (FIGS. 41, 42, 44-46) are similar in shape to those of *Microglossum*, but they are much smaller and are not multiguttulate.

Verpatinia is similar to *Mitrula*, differing in that the ascocarps arise from sclerotia. Whetzel (1945), when he described the genus, placed it in the Sclerotiniaceae, stating that the ascocarps differed from those of other genera of the family. Since they are very similar to those of species of *Mitrula*, especially *M. abietis*, the genus is included here.

In this publication, 7 species of *Microglossum*, 1 of *Spraguecola*, 3 of *Spathularia*, 4 of *Mitrula*, and 2 of *Verpatinia* have been recognized for North America. *Microglossum rufum* appears to be the most common species in eastern North America. Specimens from western North America have not been seen. *Microglossum olivaceum*, *M. fumosum*, *M. atropurpureum*, *Spraguecola irregularis*, *Spathularia flavida*, *S. velutipes*, *Mitrula paludosa* and *M. abietis* commonly occur. This study has been based mostly on specimens in the Herbarium of the University of Michigan. Where material from other herbaria has been studied it has been designated by the abbreviations recommended in the Index Herbariorum. The writer is especially indebted to Stanley Jay Smith, Lee Bonar, John A. Stevenson and Richard P. Korf for the loan of specimens.

The ascospores were studied in chloral hydrate iodine, acid fuchsin in lactophenol or nigrosin in lactophenol. Photographs of ascospores and paraphyses were mostly made from mounts in the last.



FIGS. 1, 2. *Microglossum rufum*. 1. Ascocarps, $\times 1$. 2. Squamulose stipe, $\times 3$.
 FIGS. 3, 4. *Microglossum viride*, longitudinal sections of ascocarp showing junctions
 of hymenia with stipes; 3, approx. $\times 5$; 4, approx. $\times 60$. FIGS. 5, 6. *Spraguecola*
irregularis. 5. Ascocarps of type, approx. $\times 1$. 6. E.B.M. 6002, approx. $\times 1$.
 FIG. 7. *Spathularia velutipes*, ascocarps, approx. $\times 1$.

KEY TO GENERA OF THE GEOGLOSSAEAE

1. Spores brown.....see Mains, 1954
1. Spores hyaline.....2
2. Paraphyses lacking.....*Spragueola*
2. Paraphyses present.....3
3. Ascocarps clavate, usually compressed or spatulate.....4
3. Ascocarps capitate.....5
4. Ascospores subcylindric, allantoid, subfusoid or cymbiform.....*Microglossum*
4. Ascospores acicular.....*Spathularia*
5. Ascocarps arising from sclerotia.....*Verpatinia*
5. Ascocarps not from sclerotia.....*Mitrula*

MICROGLOSSUM Gill. Disc. Champ. Fr. 25. 1879

Corynetes Hazsl. ex Durand, Ann. Myc. 6: 412. 1908.

Helote Hazsl. ex S. Ito & Imai, Proc. Jap. Assoc. Adv. Sci. 7: 145. 1932.

Ascocarps usually clavate, compressed above, yellow, orange, green, brown, olivaceous, dark purple or black, fleshy, with the hymenium confined to the upper enlarged portion; stipes smooth, furfuraceous or squamulose; asci clavate, 8-spored, + I; ascospores subcylindric, allantoid, narrowly fusoid or ellipsoid, hyaline, usually one-celled and multiguttulate, in some species rarely multiseptate; paraphyses intermixed with the asci, usually slender, straight or curved to uncinat above, usually hyaline, in one species brown.

Type: *Microglossum viride* (Pers. ex Fr.) Gill.

In his treatment Durand recognized two genera, *Microglossum* and *Corynetes*, for the species which are here placed in *Microglossum*. *Corynetes* included species which have brownish black, purplish black or black ascocarps similar to those of *Geoglossum* but with hyaline ascospores. Species having "bright colored" (yellow, orange, brown or green) ascocarps and hyaline ascospores were placed in *Microglossum*. Imai (1941) has concluded that the color differences are not sufficient for a generic separation and I agree.

Durand describes the ascospores of the species of *Microglossum* and *Corynetes* as 3-many-septate. For most species the statement is made that they are at first continuous, multiguttulate, finally multiseptate. There is considerable disagreement concerning the septation of the ascospores, the ascospores of many of the species having been described as continuous by some authors and multiseptate by others. Schroeter (1897) has grouped the species in two genera, *Microglossum* with non-

septate ascospores and *Leptoglossum* with septate ascospores. In this study septate spores have been seen in only two species, *M. longisporum* (FIG. 17) and *M. arenarium*, and in both species only a few were observed. The usual condition is what Durand has described as multiguttulate. Such spores when stained with nigrosin or acid fuchsin show variable dark staining bands with more or less guttular-like lighter areas between them (FIGS. 16, 18, 20, 21, 23). Since the bands readily take the stains they are probably bands of protoplasm. Although multiguttulate does not seem to be a very desirable term for this condition, it is used here for lack of a better.

The ascocarps of species of *Microglossum* are fairly simple in structure. They consist of more or less parallel longitudinal hyphae. There is no well-differentiated cortex in the stipe. In the outer portion of the stipe the hyphae are very compact. In the interior of the ascocarp they are looser and somewhat interwoven, becoming more so with age. The subhymenium is usually thin and is made up of compactly interwoven hyphae. The hymenium covers the enlarged upper portion of the ascocarp (FIGS. 3, 4) which is usually compressed (FIG. 1).

Durand (1908) and Corner (1930) have reported an outer veil or enclosing membrane covering the ascocarp within which the hymenium starts its development in *M. viride*. This has been demonstrated only in the very young ascocarp. It is thin, only two to four hyphae thick. According to Corner, dissolution of the hyphae of the veil occurs resulting in the formation of a mucilaginous pellicle by the time the ascocarp reaches a length of 1.5 mm. With the elongation of the ascocarp it is broken into patches and occurs only as green flecks on the stipe and hymenium and there is little or no evidence of it later in the development. Whether it occurs in other species of *Microglossum* is unknown.

Microglossum is closely related to *Geoglossum*. It has ascocarps similar in shape and structure. Most of the species of *Geoglossum* have long, brown, multiseptate ascospores while in most of the species of *Microglossum* the ascospores are hyaline, mostly multiguttulate and are much smaller. However, a few species of both *Geoglossum* and *Microglossum* have deviations which place them in an intermediate position. *Geoglossum fallax*, *G. intermedium* and *G. alveolatum* produce both brown and hyaline ascospores in variable proportions (Mains, 1954). In *G. alveolatum* the brown spores are very rare and in most collections have not been found. It has mostly multiseptate, subcylindric ascospores $(50-67-82(-95) \times 4-5 \mu$. It is therefore intermediate and is placed in *Geoglossum* on account of size and septation of ascospores and occasional production of brown spores. On the other hand *Micro-*

glossum longisporum has dimorphic hyaline ascospores (FIGS. 16, 17), the long spores $(34-60-85(-95) \times 4-5 \mu$ equalling those of *G. alveolatum*. The spores are mostly multiguttulate, less frequently septate, and brown spores are unknown. The spores of other species of *Microglossum* are shorter, mostly less than 50μ long, hyaline and mostly multiguttulate. In *M. arenarium* the multiguttulate condition is less pronounced and the paraphyses differ from those of the other species of *Microglossum*, being brown and of a type (FIG. 25) found in some species of *Geoglossum*.

KEY TO SPECIES OF MICROGLOSSUM

1. Ascospores mostly more than 50μ long or dimorphic with the long spores more than 50μ2
1. Ascospores mostly less than 50μ long.....3
2. Ascospores dimorphic, the long spores $(34-60-85(-95) \mu$, the short spores $12-22 \mu$ long.....*M. longisporum*
2. Ascospores not dimorphic, mostly more than 50μ long.
See *Geoglossum* (Mains, 1954)
3. Ascospores mostly less than 20μ long.....4
3. Ascospores mostly more than 20μ long.....5
4. Ascocarps green, stipes usually furfuraceous.....*M. viride*
4. Ascocarps predominantly brown to olivaceous, stipes smooth.....*M. olivaceum*
5. Ascocarps yellow or orange.....*M. rufum*
5. Ascocarps brown, dark purple or black.....6
6. Ascocarps yellowish brown to umber.....*M. fumosum*
6. Ascocarps brownish black, purplish black or black.....7
7. Paraphyses not or only slightly exceeding the asci, hyaline, slender, septa inconspicuous.....*M. atropurpureum*
7. Paraphyses longer than the asci, brown, robust, septa conspicuous.....*M. arenarium*

MICROGLOSSUM LONGISPORUM Durand, Ann. Myc. 6: 409. 1908.
(FIGS. 16, 17)

Helote longispora S. Ito & Imai, Proc. Jap. Assoc. Adv. Sci. 7: 147. 1932.

Type: 6-mile creek, Ithaca, N. Y. Aug. 14, 1902, Durand and Long, CUP 13524.

Ascocarps scattered or gregarious, clavate, 3-6 cm long; ascogenous portion cinnamon- to umber-brown, $\frac{1}{4}$ to $\frac{1}{2}$ the length, oblong to ellipsoid, compressed, 4-10 mm wide; stipes cinnamon-brown, terete, 2-4 mm thick, smooth or squamulose, sometimes hygrophanous or slightly viscid; asci clavate, $100-130 \times 10-12 \mu$, 8-spored; ascospores dimorphic, the long ascospores subcylindric or allantoid, slightly narrowed and rounded

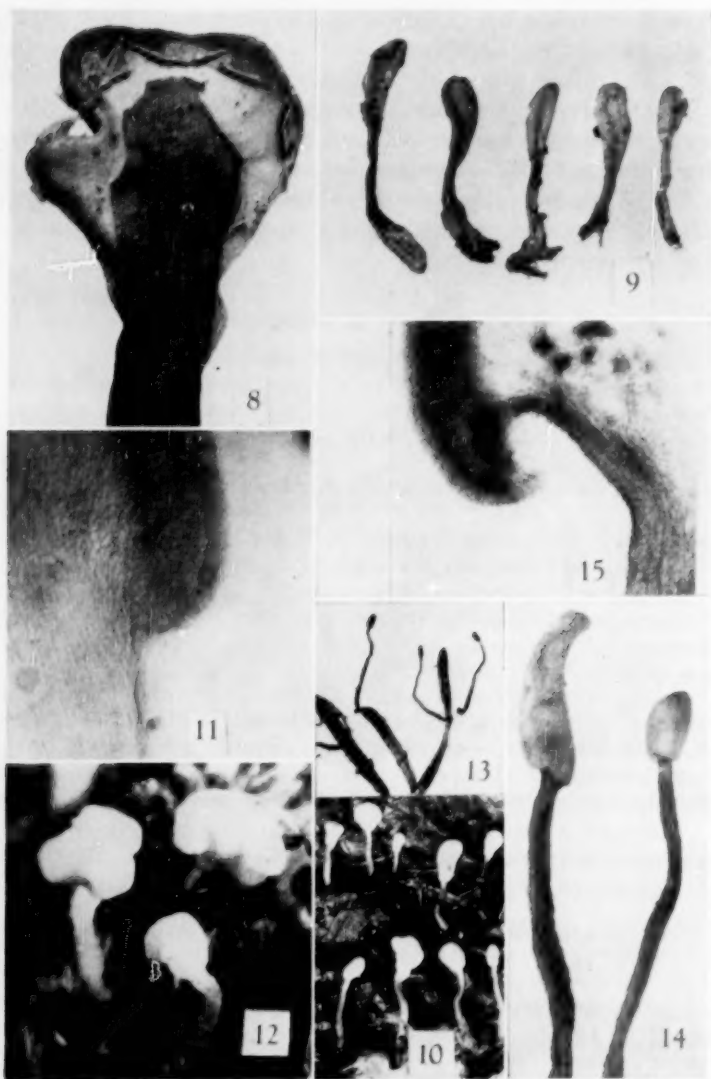


FIG. 8. *Spathularia velutipes*, showing splitting of the veil covering the hymenium, $\times 4$. FIG. 9. *Spathularia flavida* var. *ramosa*, clavate ascocarps A.H.S. 46638, $\times 1.5$. FIGS. 10, 11. *Mitrula paludosa*. 10. Ascocarps, approx. $\times 1$. 11. Longitudinal section of ascocarp showing junction of hymenium and stipe, approx. $\times 60$. FIG. 12. *Mitrula gracilis*, ascocarps, approx. $\times 5$. FIGS. 13-15. *Mitrula*

at the ends, straight or curved $(34-60-85(-95) \times 4-5 \mu$, usually multiguttulate or rarely 1-7-septate, usually 2 or sometimes 3 or 4 in an ascus, the short ascospores subcylindric, $12-22 \times 2-3 \mu$, one-celled, rarely 4 or 5, usually 6 in an ascus; paraphyses hyaline, filiform, $1-1.5 \mu$ thick below, somewhat thickened above, curved or uncinatate, with some amorphous matter, sometimes somewhat agglutinated.

On soil in rich woods and ravines.

Specimens studied: Michigan, BPI 37049. New York, CUP 1617, 13524. North Carolina, CUP 3157. Virginia, CUP 9643.

This species is known from North America only from the few specimens which are cited. It has also been reported from Japan.

M. longisporum is unique in the development of dimorphic ascospores. The long spores are longer than those of other species in the genus and approach those of some species of *Geoglossum* such as *G. alveolatum*. The absence of brown spores and the multiguttulate condition of the spores place it in *Microglossum*.

MICROGLOSSUM VIRIDE (Pers. ex Fr.) Gill. Disc. Champ. Fr. 25. 1879.
(Figs. 3, 4, 18, 19)

Geoglossum viride Pers. ex Fr. Syst. Myc. 1: 489. 1821.

Lectotype: In Persoon Herbarium at Leiden according to Durand.

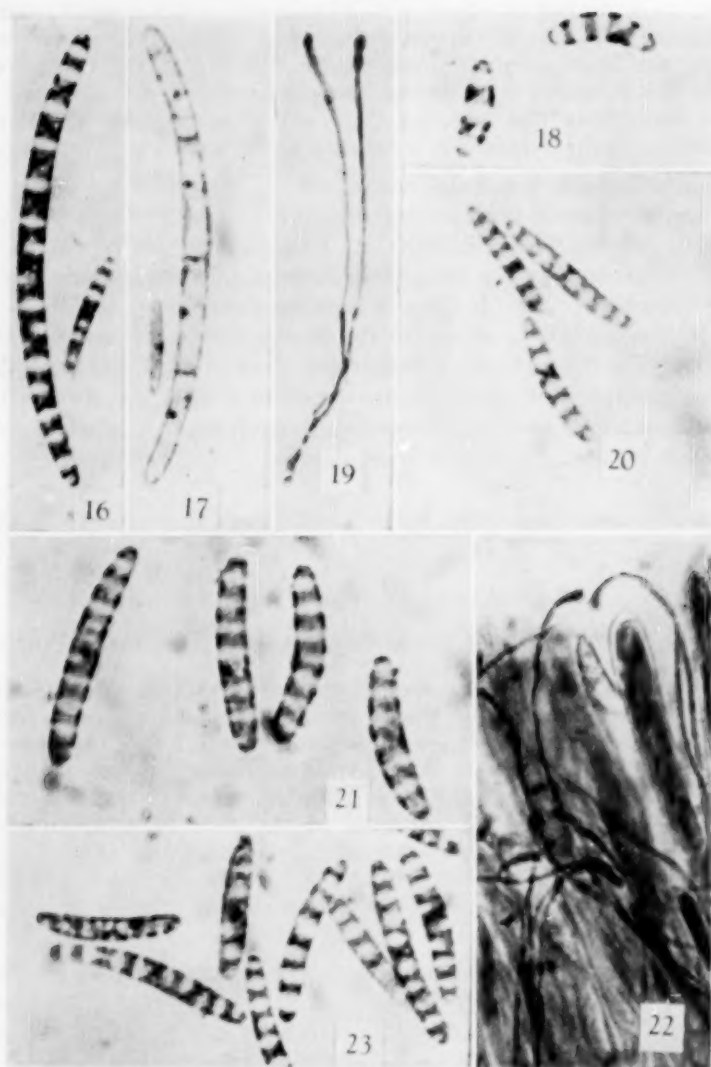
Ascocarps scattered to cespitose, clavate, 1.5-5.5 cm long; ascogenous portion $\frac{1}{3}$ to $\frac{1}{2}$ the length, compressed, 2-12 mm wide, pea-green to dark green, drying olivaceous to greenish black; stipe terete, 2-5 mm thick, concolorous, furfuraceous, becoming glabrous; asci clavate, $100-135 \times 8-12 \mu$; ascospores allantoid, subfusoid or cymbiform, $(12-)14-20(-22) \times 4-5 \mu$, one-celled, usually multiguttulate; paraphyses projecting beyond the asci, straight, branched below, filiform, $0.5-1.0 \mu$ thick below, enlarged at the apices, $1.5-2 \mu$, hyaline below, greenish above, often with green amorphous matter forming more or less of an epithecium.

On soil. In Michigan this species has been collected during August.

Specimens studied: 23 from California (MICH, UC), Michigan (MICH), New Hampshire (CUP), New York (CUP, MICH), North Carolina (CUP).

This species and *Microglossum olivaceum* are distinguished from

abietis. 13. Ascocarps, approx. $\times 1$. 14. Heads and upper portions of stipes, $\times 8$. 15. Longitudinal section of ascocarp showing sterile collar between hymenium and stipe, approx. $\times 60$.



FIGS. 16, 17. *Microglossum longisporum*. 16. Multiguttulate long and short ascospores. 17. Septate ascospores from type specimen. FIGS. 18, 19. *Microglossum viride*. 18. Ascospores. 19. Paraphysis. FIG. 20. *Microglossum atropurpureum*, ascospores. FIGS. 21, 22. *Microglossum rufum*. 21. Ascospores. 22. Paraphyses. FIG. 23. *Microglossum fumosum*, ascospores. FIGS. 19, 22, $\times 600$; others, $\times 900$.

other species of the genus by their small ascospores (FIG. 18). *M. viride* is characterized by its green color and furfuraceous stipes. Since the scales are more or less deciduous, the stipes frequently become smooth. The ascospores have been described by Durand and others as finally becoming 3-4-septate. In the specimens examined in this investigation no septate spore has been seen. The spores are commonly multiguttulate.

MICROGLOSSUM OLIVACEUM (Pers. ex Fr.) Gill. Disc. Champ. Fr. 26. 1879.

Geoglossum olivaceum Fr. Syst. Myc. 1: 489. 1821.

Microglossum contortum Peck, Bull. Torrey Bot. Club 25: 328. 1898.

Microglossum obscurum Peck, Bull. Torrey Bot. Club 26: 71. 1899.

Ascocarps scattered to cespitose, clavate, sometimes twisted and contorted, 1-6 cm long; ascogenous portion $\frac{1}{3}$ to $\frac{1}{2}$ the length, compressed, 3-10 mm wide, olivaceous, olivaceous buff, smoky buff, chestnut, walnut-brown, drying reddish brown to black; stipe terete, 1-4 mm thick, olivaceous, olive-buff, pallid buff, ocher, pallid wood-brown, drying dark brown to black, smooth; asci clavate, 70-100 \times 7-10 μ ; ascospores subfusoid, cymbiform or allantoid, 10-18(-20) \times 3.5-5 μ , one-celled, usually multiguttulate; paraphyses projecting beyond the asci, straight, branched below, filiform, 0.5-1 μ thick below, somewhat enlarged at the apices, 1.5-2 μ , hyaline below, hyaline or greenish above, often with greenish or brownish amorphous matter forming more or less of an epithecium.

On soil. In Michigan this species has been collected from July 30 to October 31.

Specimens studied: 46 from California (UC, MICH), Connecticut (CUP), District of Columbia (CUP), Michigan (MICH), New York (CUP, UC), Ohio (MICH), Oregon (MICH), Vermont (CUP), Washington (MICH), Virginia (CUP), Ontario (CUP, MICH).

Microglossum olivaceum is very closely related to *M. viride*, from which it can best be distinguished in the fresh condition. In color the ascocarps are brown or some combination with brown. The olivaceous variants approach the nearest to *M. viride*. When dried the species are even less distinctive. Although septate spores have been described for this species, none has been seen in this study.

Mitrula bermudiana Waterston (1945) probably belongs here. It was described from two collections (CUP 33211 and CUP 33212, type) collected in Bermuda. Together they contain four small ascocarps of

which only one has asci and ascospores. The mature ascocarp is clavate. A note states that the color was hygrophorous tan. It now is brownish black. The ascospores are subfusoid, allantoid or narrowly cymbiform, $10-16 \times 4 \mu$, and multiguttulate. The clavate ascocarp and the multiguttulate ascospores indicate that this is a *Microglossum*.

MICROGLOSSUM RUFUM (Schw.) Underw. Minn. Bot. Studies 1: 496. 1896. (Figs. 1, 2, 21, 22)

Geoglossum rufum Schw., Trans. Am. Phil. Soc. 4: 181. 1834.

Geoglossum luteum Peck, Rep. N. Y. State Mus. 24: 94. 1872.

Type: From New Jersey, in the herbarium of the Philadelphia Academy of Natural Sciences according to Durand.

Ascocarps scattered to cespitose, clavate, 2-7 cm long, yellow to orange, drying brownish orange or sometimes yellowish or reddish brown; ascogenous portion $\frac{1}{4}$ to $\frac{1}{2}$ of the length, compressed, 4-12 mm wide; stipe terete, 2-4 mm thick, prominently squamulose; asci clavate, $100-135 \times 9-12 \mu$; ascospores subcylindric or allantoid, $(18-20-36(-40) \times 4-6 \mu$, mostly multiguttulate, straight or curved, narrowed somewhat and rounded at the ends; paraphyses slightly projecting beyond the asci, filiform, slightly enlarged at the apices, mostly strongly curved or uncinatate, branched below, hyaline, sometimes with hyaline amorphous matter above.

In *Sphagnum*, moist and dry soil and on rotten wood. Collected in Michigan from June 30 to September 7.

Specimens studied: 131 from Alabama (MICH), Connecticut (CUP), Louisiana (CUP), Maine (CUP), Massachusetts (CUP), Michigan (MICH), New Hampshire (CUP, UC), New York (CUP, UC), North Carolina (CUP), South Carolina (CUP), Tennessee (UC), Vermont (CUP), Virginia (CUP), Wisconsin (CUP), Ontario (CUP, MICH).

This is the most abundant species of *Microglossum* in North America. In the fresh condition it is easily distinguished by its yellow or orange color and by the conspicuously squamulose stipes (FIG. 2).

The scales of the stipe consist of a compact mass of subglobose to subellipsoid cells, $6-10 \times 6-8 \mu$, much shorter and wider than the cylindrical cells, $22-34 \times 3-4 \mu$, of the hyphae of the stipe underlying them. In some instances the scales curve outward both above and below their attachment to the stipe, suggesting that they may have been formed by ruptures of an outer layer during the elongation of the stipe. Some-

times also, the underlying hyphae of the stipe may also be ruptured and form part of the scale.

MICROGLOSSUM FUMOSUM (Peck) Durand, Ann. Myc. 6: 408. 1908.
(Fig. 23)

Leptoglossum fumosum Peck, Bull. N. Y. State Mus. 116: 25. 1907.

Type: Sandlake, N. Y. Aug. C. H. Peck (NYS).

Ascocarps scattered to cespitose, clavate, 2-8 cm long, light yellowish brown, cinnamon-brown, ochraceous tawny, dark buff, umber, usually drying dark brown; ascogenous portion $\frac{1}{3}$ to $\frac{1}{2}$ the length, compressed, 3-15 mm wide; stipe terete, 2-5 mm thick, furfuraceous, becoming smooth; asci clavate, $100-150 \times 8-12 \mu$; ascospores subcylindric or allantoid $(16-20-40(-48) \times 4-5 \mu$, usually multiguttulate, straight or curved, narrowed somewhat and rounded at the ends; paraphyses not or slightly projecting beyond the asci, filiform, $1-2 \mu$ thick below, slightly thickened at the apices, $2-4 \mu$, strongly curved to uncinatate above, hyaline, often with amorphous matter forming a slight epithecium.

On soil and rotting wood. Collected in Michigan from July 11 to September 14.

Specimens studied: 46 from Massachusetts (CUP, MICH), Michigan (MICH), New York (CUP, UC), Pennsylvania (NY), Washington (MICH).

Microglossum fumosum differs from *M. rufum* principally in the color of the ascocarps. The stipes are not as squamulose as in that species and the ascospores are slightly larger. The scales of the stipe are smaller but similar in structure to those of *M. rufum*.

There is some question whether *Geoglossum pistillaris* Berk. & Cooke is this species or *M. rufum* as given by Durand and others. The color is described (Cooke, 1879) as rufescens. As illustrated, the ascocarps are yellowish brown and the stipes smooth. The illustration is more characteristic of *M. fumosum* than *M. rufum*. The publication of *M. pistillaris* antedates *M. fumosum*. However, since the illustrations were made from dried specimens the color when fresh is uncertain and the application of the name *M. pistillaris* is very doubtful.

MICROGLOSSUM ATROPURPUREUM (Batsch ex Fr.) Karsten, Acta Soc. Fauna Flora Fenn. 2, no. 6: 110. 1885. (Fig. 20)

Geoglossum atropurpureum Fr., Syst. Myc. 1: 490. 1821.

Geoglossum microsporum C. & Pk., Ann. Rep. N. Y. State Mus. 25: 97. 1873.

Corynetes purpurascens Durand, Ann. Myc. 6: 413. 1908.

Corynetes atropurpureus Durand, Ann. Myc. 6: 414. 1908.

Corynetes robustus Durand, Ann. Myc. 6: 416. 1908.

Microglossum robustum Smith & Ramsb., Trans. British Myc. Soc. 4: 320. 1913.

Lectotype in the Persoon Herbarium at Leiden according to Durand.

Ascocarps clavate 1-7 cm long; ascogenous portion $\frac{1}{3}$ to $\frac{1}{2}$ the length, compressed, 2-15 mm wide, dark brown, purplish black or black; stipe terete, 2-8 mm thick, brownish black or black, smooth or minutely squamulose; asci clavate, $90-150 \times 8-14 \mu$; ascospores subcylindric or allantoid $(16-20-44(-52) \times 4-6 \mu$, one-celled, multiguttulate, somewhat narrowing and rounded at the ends, straight or slightly curved; paraphyses not or slightly projecting beyond the asci, straight or slightly curved above, hyaline, filiform, not or slightly enlarged at the apices, sometimes agglutinated with amorphous matter forming more or less an epithecium.

On soil. In Michigan collected from August 6 to September 22.

Specimens studied: 53 from Maine (CUP), Massachusetts (CUP), Michigan (MICH), Mississippi (CUP), New Hampshire (MICH, NY, CUP), New York (CUP, MICH), New Jersey (CUP), Oregon (MICH), North Carolina (CUP, MICH), Tennessee (T), Virginia (CUP), Washington (MICH), Quebec (MICH), Nova Scotia (MICH).

Microglossum atropurpureum as presented here includes three species, *Corynetes atropurpureus*, *C. purpurascens* and *C. robustus* as treated by Durand. He distinguished *C. purpurascens* from *C. atropurpureus* on the basis of having a more distinctly purplish tint of the fresh plant and more abruptly thickened tips to the paraphyses. There is considerable variation in these characters and they are not sufficient to justify specific separations. Durand, in describing *C. robustus*, noted its close relationship to *C. atropurpureus*. He places greatest emphasis upon a lack of an epithecium and paraphyses slightly thickened and curved at the tips in distinguishing *C. robustus* from *C. atropurpureus*. There is considerable variation in the development of the brown amorphous layer which he describes for the epithecium of *C. atropurpureus*. It occurs to a moderate extent in the type of *C. robustus*. There is also variation in the paraphyses. Straight to curved paraphyses frequently occur together. It seems best to unite these in one species.

MICROGLOSSUM ARENARIUM Rostrup, Med. om Grønland 3: 606. 1891.
(Figs. 24, 25)

Leptoglossum latum Peck, Bull. Torrey Bot. Club 22: 210. 1895.

Corynetes arenarius Durand, Ann. Myc. 6: 417. 1908.

Type: East Greenland, N. Klartz, Aug. 1890 in Rostrup Herbarium, Copenhagen, Denmark, according to Durand.

Ascocarps scattered to cespitose, clavate, 1-5 cm long, brownish black to black; ascogenous portion $\frac{1}{2}$ to $\frac{3}{4}$ of the length, compressed, 2-15 mm wide; stipes terete, 1-3 mm thick, squamulose, asci clavate, $110-145 \times 12-16 \mu$; ascospores subcylindric to allantoid, $(25-28-42(-45) \times 4-6 \mu$, one-celled or rarely 1-septate, sometimes multiguttulate, straight or curved, narrowed and rounded at the ends; paraphyses longer than the asci, very variable, mostly curved to uncinatate above, light to dark brown, $2-3 \mu$ wide below, $3-14 \mu$ at the apices, the septa conspicuous.

On soil. Collected in Michigan from August 10 to September 24.

Specimens studied: Michigan, A. H. Smith 33262, 34192, 37605, 37607 (MICH). Greenland, N. Klartz, from type (CUP 2499). Labrador, A. C. Waghorne (type of *Leptoglossum latum* NYS, also CUP 993, 3063, 5430). Newfoundland, A. C. Waghorne (CUP 3062).

This species has also been reported from Denmark and Japan.

The paraphyses (FIG. 25) distinguish this species from others in *Microglossum*. They are brown, longer than the asci and on account of the brown walls the septa are conspicuous. They vary considerably in thickness and in shape.

The Michigan collections differ somewhat from the others. The paraphyses are lighter brown and the ascocarps are slender. The differences do not appear sufficient to separate them.

The scales of the stipe appear to be formed from a layer of hyphae somewhat similar to the paraphyses. They agglutinate together to form the scales. This is similar to the condition found in *Geoglossum fallax*.

This species approaches those in *Geoglossum* which produce hyaline spores in part. The paraphyses resemble more those produced in some species of *Geoglossum* than those of other species of *Microglossum*. However, brown spores have not been noted for *M. arenarium* and their size is more in agreement with that found in *Microglossum*.



FIGS. 24, 25. *Microglossum arenarium*. 24. Ascospores. 25. Paraphyses. FIG. 26. *Spragueola irregularis*, ascospores. FIGS. 27, 28. *Spathularia flavida* var. *tortuosa*. 27. Ascospores. 28. Paraphyses. FIGS. 29, 30. *Spathularia flavida* var. *ramosa*. 29. Asci. 30. Ascospore with attached conidia. FIGS. 25, 28, 29, $\times 600$; others, $\times 900$.

SPRAGUEOLA Massee, Jour. Bot. 34: 150. 1896.

Ascocorynium S. Ito & Imai, Trans. Sapporo Nat. Hist. Soc. 13: 179. 1932.

Ascocarps clavate, irregular, twisted, contorted or lobed, fleshy or fleshy-leathery, stipitate or sessile; hymenium covering the upper portion or rarely all of the ascocarp; stipe slender to robust, sometimes very short; ascospores ellipsoid, 1-celled, hyaline; paraphyses absent.

Type: *Spragueola americana* Massee (= *S. irregularis* (Peck) Nannf.).

The ascocarps have a simple structure. They consist of more or less longitudinal hyphae which are compact to the outside of the stipe and looser and more interwoven in the interior of the stipe and the upper ascogenous portion of the ascocarp. The subhymenium is made up of densely interwoven hyphae.

Spragueola differs from the other genera of the Geoglossaceae in the absence of paraphyses in the hymenium. The ellipsoid ascospores (Fig. 26) are also distinctive. Two species, *S. irregularis* and *S. vitellina* (Bres.) Nannf., have been recognized for the genus. They have been treated by Durand and others as species of *Mitrula* Imai (1941) has recognized the genus as distinct but rejects the name *Spragueola* because he considers the type species is based on an abnormal and monstrous specimen. However, *S. irregularis* is a species having very variable ascocarps and the type of *S. americana* is one of the extreme variations. It therefore is not a monstrosity in the sense of article 77 of the International Code of Botanical Nomenclature and I agree with Nannfeldt that *Spragueola* is the valid name for the genus.

SPRAGUEOLA IRREGULARIS (Peck) Nannf., Ark. Bot. 30A, No. 4: 57. 1942. (Figs. 5, 6, 26)

Geoglossum irregulare Peck, Rep. N. Y. State Mus. 32: 45. 1879.

Mitrula luteola Ellis, Am. Nat. 17: 192. 1883.

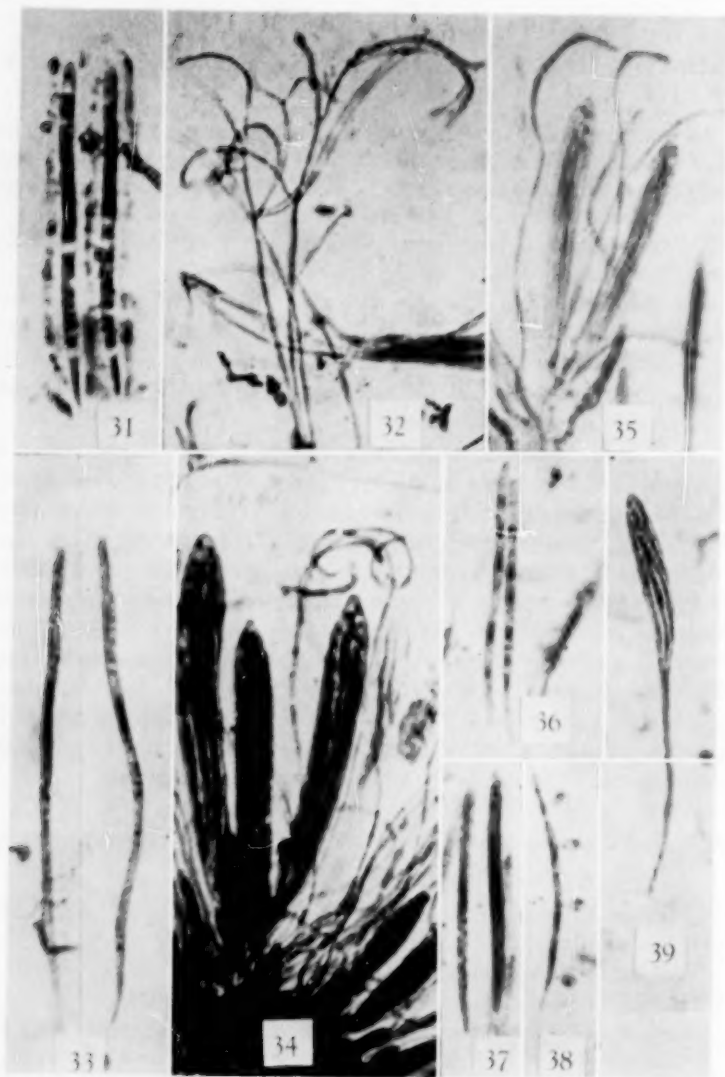
Spragueola americana Mass., Jour. Bot. 34: 150. 1896.

Mitrula irregularis Durand, Ann. Myc. 6: 398. 1908.

Ascocorynium irregulare Imai, Trans. Sapporo Nat. Hist. Soc. 13: 179. 1934.

Type: Sandlake, N. Y. C. H. Peck in the Herbarium of the N. Y. State Museum.

Ascocarps crowded or cespitose or rarely scattered, very variable, clavate, contorted, twisted, lobed or branched, often compressed, stipitate or sometimes sessile, 1-7 cm long; ascogenous portion occupying the upper portion or sometimes all of the ascocarp, 2-15 mm wide,



FIGS. 31, 32. *Spathularia flavida* var. *ramosa*. 31. Ascospores showing gelatinous walls. 32. Paraphyses. FIGS. 33, 34. *Spathularia flavida* var. *longispora*. 33. Ascospores. 34. Asci and paraphyses. FIGS. 35, 36. *Spathularia flavida* var. *brevispora*. 35. Immature asci and paraphyses. 36. Ascospores. FIGS. 37, 38. *Spathularia velutipes*. 37. Ascospores. 38. Ascospore with attached conidia. FIG. 39. *Spathularia spathulata*, ascus. FIGS. 32, 34, 35, 39, $\times 600$; others, $\times 900$.

lemon-, apricot-, cadmium- or orange-yellow; stipes, 2-8 mm thick, white; asci clavate, $60-125 \times 5-6 \mu$, occurring as groups of branches from ascogenous cells; ascospores ellipsoid, sometimes slightly flattened on one side, $(4-)6-8(-10) \times 3-4 \mu$, 1-celled; paraphyses absent.

On ground and in moss, especially under conifers. Collected in Michigan from July 25 to September 19.

Specimens studied: 56 from Colorado (MICH), Connecticut (CUP), District of Columbia (CUP), Maine (FH, CUP, MICH), Maryland (CUP), Massachusetts (CUP), Michigan (MICH), Montana (MICH), New Hampshire (FH, MICH), New Jersey (MICH), New York (MICH, CUP, FH, NYS), North Carolina (MICH), Oregon (MICH), Tennessee (MICH, FH, CUP), Vermont (FH), New Brunswick (CUP), Nova Scotia (CUP), Ontario (MICH, FH, CUP).

This species has also been reported from Japan by Imai. Durand reported it from North America as *Mitrula irregularis* and *M. vitellina*.

It is an unique species. The ascocarps are very variable. In some collections they are more or less clavate and stipitate (Fig. 6). In most collections they are very variable and may be stipitate and sessile, clavate and variously contorted, twisted and lobed (Fig. 5). *Spragueola americana* was based on a collection of sessile ascocarps. In *S. irregularis* paraphyses are lacking and the hymenium consists entirely of asci which in crushed mounts separate as groups of branches from ascogenous cells.

Spragueola vitellina (Bres.) Nannf. was described by Bresadola (1882) as *Geoglossum vitellinum* from the Tyrol, Italy. He gives the ascocarps as lanceolate and the ascospores as obovate, $7-8 \times 4 \mu$, and states that paraphyses rarely occur. A specimen from Bresadola at Cornell (CUP 507) agrees with his description and illustration except that paraphyses do not occur. Durand has reported a specimen of this species as *Mitrula vitellina* from Rugby, Tenn. He distinguished it from *M. irregularis* by the regularly clavate ascocarps and smaller ascospores, $4-6 \times 3-4 \mu$ as compared with $6-10 \times 4-5 \mu$ for *M. irregularis*. Its spores are therefore also smaller than those of *Geoglossum vitellinum*. The ascospores of the type specimen of *Geoglossum irregulare* Peck (NYS) are $4-8 \times 3-4$, mostly $5-6 \times 3 \mu$. The differences in spore size are therefore not significant. It seems doubtful whether the clavate condition distinguishes a separate species. Collections show considerable differences in variability and commonly include clavate variants. Some are mostly clavate. The latter apparently represent one extreme of the variability of the species and the type of *Spragueola americana* the other. Whether *Spragueola vitellina* is a distinct species is ques-

tionable. More information concerning its occurrence and variation in Europe is necessary in order to determine its status.

SPATHULARIA Fr., Sys. Myc. 1: 490. 1821.

Mitruliopsis Peck, Bull. Torrey Bot. Club 30: 100. 1903.

Ascocarps fleshy or fleshy-leathery, spathulate or rarely compressed-capitate; ascogenous portion covering the upper portion of the ascocarp, very compressed, fan-shaped, decurrent on opposite sides of the stipe or rarely somewhat capitate; stipe terete; asci clavate, — I; ascospores acicular, usually 1-celled or less frequently several-septate, in two species producing conidia on short sterigmata; conidia subglobose to obovoid, hyaline, 1-celled, sometimes replacing the ascospores and filling the asci; paraphyses filiform, simple or branched below, curved to circinate above, hyaline.

Type: *Spathularia flavida* Fr.

This genus is distinguished from *Microglossum* by the acicular ascospores (Figs. 27, 31, 33, 36, 37, 40) and usually by the spathulate ascocarps (Fig. 7). However, in *S. flavida* var. *ramosa* ascocarps may be produced which are compressed-clavate as in *Microglossum* (Fig. 9). There is considerable evidence for a fairly close relationship with *Cudonia* in the Cudonieae. *Cudonia* has a parallel development of species. The ascospores are acicular and have a similar production of conidia in some species. However, *Cudonia* has pileate ascocarps with the underside of the pileus sterile. *Spathularia spathulata*, which was described in *Cudonia*, has ascocarps which vary from spathulate to capitate but with the hymenium completely covering the head.

The stipes of the ascocarps of species of *Spathularia* consist of more or less longitudinal hyphae which in the center are loosely interwoven and toward the outside become more compact. The hyphae continue upward and in the ascogenous portion of the ascocarp are very loosely interwoven except for the narrow, very compact subhymenial layer, which consists of closely interwoven hyphae. The hymenium, consisting of asci and paraphyses, covers the upper part of the ascocarp. In one species, *S. velutipes*, the hymenium is covered by a well-developed veil (Fig. 8) which also is the outer layer of the stipe. With the development and expansion of the ascogenous portion of the ascocarp the covering veil breaks into fragments and the hymenium is exposed. The development of this species has been described by Duff (1922). Such a veil has not been noted for the other species. *S. flavida* has a thin layer of interwoven hyphae covering the stipe, which may indicate

that the hymenium is similarly covered in the early stages of development of the ascocarp.

Ascospores commonly produce conidia which are borne on short sterigmata (Figs. 30, 38). Conidial production may occur in the asci and conidia may replace the ascospores. The production of conidia by ascospores has not been noted elsewhere in the Geoglosseae. It occurs in the Cudoniace and appears to be somewhat similar to that found in *Coryne*.

KEY TO THE SPECIES OF SPATHULARIA

1. Ascospores 18-26 μ long.....*S. spathulata*
1. Ascospores mostly more than 30 μ long.....2
2. Stipes whitish, yellowish or light brown, smooth or byssoid; mycelium white or yellowish.....*S. flavida*
2. Stipes dark brown, farinaceous; mycelium orange.....*S. velutipes*

SPATHULARIA FLAVIDA Fr., Sys. Myc. 1: 491. 1821. (Figs. 9, 27-36)

Mitruliopsis flavida Peck, Bull. Torrey Bot. Club 30: 100. 1903.

Ascocarps cespitose, gregarious, or scattered, sometimes growing in circles, spathulate or rarely compressed-clavate, 1-8 cm long, arising from a whitish or pale yellow mycelium; ascogenous portion usually much compressed, rarely flattened clavate, up to 3 cm wide, more or less decurrent on opposite sides of the stipe, smooth, undulate, rugose, sometimes lobed or contorted, light yellow to cinnamon-buff; stipe terete or somewhat compressed above, whitish, pale yellow to cinnamon-buff, glabrous, thinly byssoid or matted-tomentose; asci clavate, 85-125 \times 8-12 μ ; ascospores acicular, rounded above, acuminate below, very variable in size, 30-95 \times 1.5-2.5 μ , 0-several-septate, commonly continuous, the wall with a gelatinous layer swelling to 1.5-3 μ thick; conidia subspherical, ellipsoid or obovoid, 1-2 \times 1-1.5 μ , 1-celled, hyaline, produced by the ascospores on sterigmata, sometimes replacing the ascospores and filling the asci; paraphyses filiform, simple or branched below, not or irregularly branched above, strongly curved or circinate or straight above, hyaline (see varieties).

On humus and rotten wood. Collected in Michigan from July 18 to October 11.

SPATHULARIA FLAVIDA var. **flavida**.

Ascospores (40-)45-56(-62) \times 2-2.5 μ ; paraphyses not or slightly branched above, curved to circinate at the apices.

Specimens studied: 9 from Idaho, Michigan, New York, Oregon, Washington, Ontario (all MICH).

Information is not available concerning the ascospores and paraphyses of the collections upon which Fries based *Spathularia flavida*. The European specimens (Syd. Myc. germ. 1643, 2541, Rehm Asco. 426b, Starcs 2689, Lohwag 710) which have been seen have ascospores and paraphyses as described above and it is assumed the description applies to the typical variety.

S. FLAVIDA var. **tortuosa** var. nov. (FIGS. 27, 28)

Var. *flavida* simile sed paraphysibus supra circinatis vel tortuosis.

Type: Rees' Bog, University Michigan Biological Station, Cheboygan Co., Michigan, Sept. 22, 1949, A. H. Smith 34133.

Specimens studied: 7 from Idaho and Michigan (all MICH).

Variety *tortuosa* is similar in the size of the ascospores (FIG. 27) to var. *flavida*. The paraphyses are much more curved to circinate and twisted at the apices (FIG. 28), often forming a dense intertwined layer above the asci.

S. FLAVIDA var. **ramosa** var. nov. (FIGS. 29-32)

Var. *flavida* simile sed paraphysibus supra irregulare, multum ramosis.

Type: Papoose Creek, Seven Devils Mts., Idaho, Aug. 23, 1954, A. H. Smith and H. E. Bigelow, 46638.

Specimens studied: 7 from Idaho, Michigan, Oregon (all MICH).

Variety *ramosa* has ascospores (FIG. 31) similar in size to var. *flavida*. The paraphyses (FIG. 32) differ considerably, being mostly irregularly much-branched above, the branches straight or somewhat curved. The ascocarps of this variety show considerable variation from typical spathulate to a clavate, slightly flattened condition. In the type all the ascocarps are compressed-clavate (FIG. 9), resembling those of a *Microglossum*. *S. minima* Maire (1901) is described and illustrated as having paraphyses densely branched above. The ascospores are given as smaller, $39-42 \times 1.5-2 \mu$.

S. FLAVIDA var. **brevispora** var. nov. (FIGS. 35, 36)

Var. *flavida* simile sed ascosporis $(30-35-45(-50) \times 1.5-2 \mu$.

Type: Tahquamenon Falls, Michigan, Sept. 2, 1949, A. H. Smith, 33231.

Specimens studied: 31 from Michigan, Washington, Nova Scotia, Ontario (all MICH).

Variety *brevispora* has paraphyses (FIG. 35) similar to those of var. *flavida*. Its ascospores are shorter (FIG. 36). Of the collections studied, 25 are from Michigan, where it is the most common variety. *S. flavida* var. *alpestris* Rehm (Rehm Asco. no. 1551) is similar to this variety. It has ascospores $32-40(-45) \times 2 \mu$ and paraphyses which are curved or circinate at the apices. Rehm stresses the small size of the ascocarps and the lilac-pruinose condition. As previously stated, *S. minima* has small ascospores but the paraphyses are simple above.

S. FLAVIDA var. *longispora* var. nov. (FIGS. 33, 34)

Var. *flavida* simile sed ascosporis $(50-)55-75(-85) \times 2-2.5 \mu$.

Type: Mt. Angeles, Olympic Mts., Washington, Sept. 21, 1941, A. H. Smith, 17112.

Specimens studied: 8 from California, Idaho, Oregon, Washington (all MICH).

Variety *longispora* has paraphyses (FIG. 34) similar to var. *flavida*. Its ascospores (FIG. 33) are much longer. *S. neesii* Bres. is similar to this variety in spore length. There is some uncertainty concerning its paraphyses. Bresadola (1881) illustrates them branched above. Rehm (1896) describes them as "hakig" above. Two specimens have been seen, Rehm Asco. nos. 1256 and 1256b. In no. 1256, collected by Bresadola, the paraphyses are so agglutinated that their branching could not be determined. In no. 1256b, collected by v. Höhnelt, they are simple above and curved to circinate at the apices. The ascospores are $40-60 \times 2.5 \mu$. This appears to be *S. flavida* var. *flavida*.

No evidence of a "veil" over the hymenium as occurs in *S. velutipes* has been seen in *S. flavida*. The stipe is covered by a thin layer of closely interwoven narrow hyphae with many separate outward-projecting short hyphae which give the byssoid to tomentose appearance to the stipe. It is possible that this outer layer may continue over the hymenium in early stages of the development, but if so it probably disappears early in the development of the ascocarp.

The walls of the ascospores (FIG. 31) are more or less gelatinous. This can be demonstrated best by treatment with chloral hydrate-iodine. The gelatinous condition brings about an adherence and clumping of the spores.

Conidia (FIG. 30) occur abundantly in some collections. Several may be produced on short sterigmata by an ascospore. Sometimes they replace the ascospores and fill the asci.

The species is very variable in size and color of ascocarps, in size

of ascospores and in branching of paraphyses. In Europe *S. rufa* Swartz, *S. badipes* Pat., *S. nigripes* Quél., *S. neesii* Bres. and *S. flavida* var. *alpestris* Rehm have been distinguished from *S. flavida* mostly on account of differences in size and color of the ascocarps. The importance of these criteria is doubtful and these taxa have not been recognized in this study. Differences in size of ascospores appear to have greater significance. Although there is intergradation, collections can be separated into short-spored, (30-)35-45(-50) μ , medium-spored, (40-)45-56(-62) μ , and long-spored, (50-)55-75(-85) μ groups. Most have spores of medium length. In most collections the paraphyses are curved to circinate at the apices. In such collections they may have short, medium or long ascospores. In some the curving of the paraphyses is greatly accentuated and they are circinate to considerably twisted and intertwined to form a tangled layer above the asci. The ascospores are of medium length. Although the paraphyses of most collections appear simple, they are frequently somewhat branched at the base. In some collections, however, they are bushy, due to repeated irregular branching above. The latter have ascospores of medium size.

It seems best to recognize these variants as varieties of *S. flavida*. In Europe *S. minima* has ascospores $39-42 \times 1.5-2 \mu$ and paraphyses much-branched above and *S. neesii* has ascospores $60-80 \times 1.5-2 \mu$ and paraphyses branched above. According to the treatment followed here they should be varieties *S. flavida* var. *minima* (Maire) comb. nov. (*S. minima* Maire, Bull. Soc. Bot. France 48: CCH 1901) and *S. flavida* var. *neesii* (Bres.) comb. nov. (*S. neesii* Bres. Fungi trid. 66, 1884). These varieties probably occur in north America.

SPATHULARIA VELUTIPES Cooke & Farl., Grevillea 12: 37. 1883.
(Figs. 7, 8, 37, 38)

Type in the Kew Herbarium according to Durand.

Ascocarps gregarious or cespitose or rarely scattered, spatulate, up to 6 cm long, arising from an orange mycelium; ascogenous portion much compressed, up to 3 cm wide, fan-shaped, decurrent on opposite sides of the stipe; smooth, rugose, lobed or contorted, whitish, cream or light brownish yellow, with fragments of the veil commonly remaining at the juncture with the stipe or as patches on the hymenium; stipe terete or somewhat compressed above, 3-8 mm thick, up to 4 cm long, light to dark brown, farinaceous; asci clavate, $75-110 \times 8-10 \mu$; ascospores acicular, rounded above, acuminate below, $(26-)30-42(-46) \times 1.5-2 \mu$, 0-several-septate, commonly continuous, the wall showing a gelatinous layer $1.5-2 \mu$ thick; conidia subspherical, ellipsoid or obovoid,

2.5–3 × 2–2.5 μ , one-celled, produced on short sterigmata on the ascospores, frequently replacing the ascospores and filling the asci; paraphyses filiform, simple or branched below, strongly curved or circinate above, hyaline.

On rotting wood and humus. Collected in Michigan from July 19 to September 5.

Specimens studied: 38 from Michigan, New Hampshire, New York, North Carolina, Tennessee, Ontario (all MICH).

S. velutipes differs from *S. flavida* in the orange mycelium and dark brown farinaceous stipe and in the well-developed veil which often persists along the margin of the hymenium or less frequently as patches on the hymenium (FIG. 8). The veil over the hymenium is a continuation of an outer layer covering the longitudinal hyphae of the stipe. It is a 30–50 μ thick, compact layer of hyaline- and brown-walled cells. Within, it consists of small (4–5 μ) cells with thin hyaline walls and is without intercellular spaces. The outer portion is made up of somewhat larger cells with thicker, brown, rough walls. The outer portion is variously split into wedge- or irregular-shaped masses of brown cells which give the farinaceous condition to the stipe and patches of veil on the hymenium.

The ascospores of *S. velutipes* fairly commonly produce conidia on short sterigmata (FIG. 38) and many collections have asci filled with the conidia. Durand states that the ascospores of *S. velutipes* are 33–43 μ long and the specimens examined in this study are in agreement.

***Spathularia spathulata* (Imai) comb. nov. (FIGS. 39, 40)**

Cudonia spathulata Imai, Bot. Mag. 56: 524. 1942.

Type: Big Basin, Santa Cruz Co., California, February 22, 1931, H. E. Bailey, UC 439652.

Ascomcarps spathulate, irregularly compressed, capitate or flattened-capitate, up to 3 cm long, stipitate, fleshy; ascogenous portion much-compressed to irregularly subglobose, decurrent on opposite sides of stipe or with the hymenium completely covering the subglobose heads, 5–12 mm wide, rugose, yellow-brown to reddish brown; stipe 1.5–5 mm wide, brownish yellow to reddish brown; asci clavate, 90–110 × 6–8 μ ; ascospores acicular, 18–26 × 2 μ , usually 1-celled or rarely septate, somewhat gelatinous; paraphyses exceeding the asci, branched below, filiform, circinate (described entirely from the dried specimen).

Known only from the type specimen.

Imai described this as a species of *Cudonia*. However, it is not pileate with the lower surface of the pileus sterile as in *Cudonia*. The ascocarps vary from spathulate to capitate. Since the species is known only from the one collection, the significance of the deviation from the spathulate condition cannot be evaluated. The capitate variants are

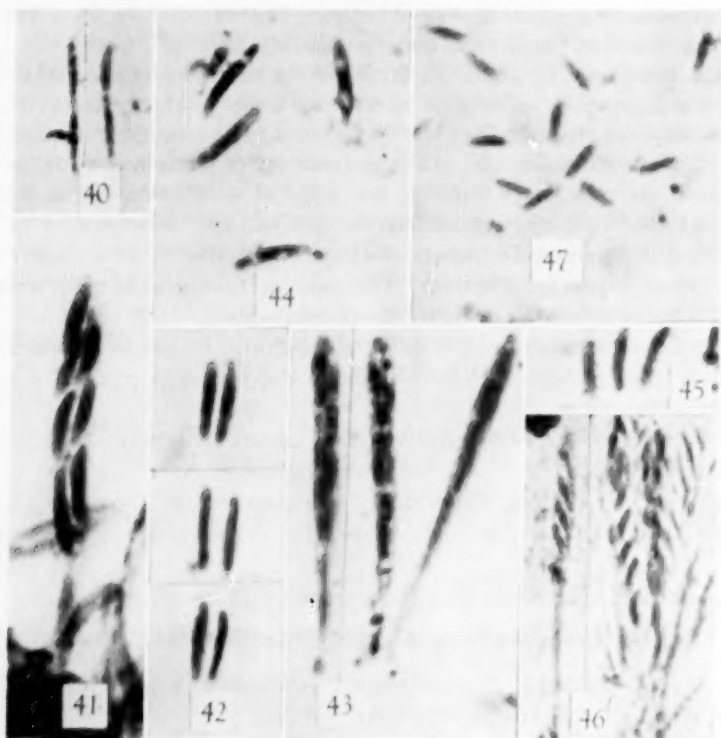


FIG. 40. *Spathularia spathulata*, ascospores. FIGS. 41, 42. *Mitrula paludosa*. 41. Ascus. 42. Ascospores. FIGS. 43, 44. *Mitrula abietis*. 43. Asci. 44. Ascospores. FIG. 45. *Mitrula gracilis*, ascospores. FIG. 46. *Mitrula morchelloides*, asci and ascospores. FIG. 47. *Verpatinia calthicola*, ascospores. All $\times 900$.

fertile over the entire surface. The short spores (FIG. 40) and asci attenuated below (FIG. 39) distinguish it from other species of the genus, and in these respects it resembles some of the species of *Cudonia*.

Whether a veil occurs in this species is uncertain. There is a thin (25μ) layer on the outside of the stipe of very densely interwoven

hyphae from which short scattered hyphae project outward. No evidence that this layer continues over the hymenium has been found. However, it may have been destroyed in the early stages of the development of the ascocarp.

MITRULA Fr., Syst. Myc. 1: 491. 1821.

Gymnomitrula Imai, Jour. Faculty Agr. Hokkaido Imp. Univ. 45: 172. 1941.

Ascocarps small, capitate or subcapitate with the hymenium more or less sharply delimited, stipitate, bright colored; asci clavate, + I; ascospores subfusoid, cymbiform, subfalcate, subcylindric or clavate, one-celled or rarely 1-septate, hyaline; paraphyses present.

Type: *Mitrula paludosa* Fr.

Durand included *M. irregularis*, *M. vitellina*, *M. phalloides* (= *M. paludosa*), *M. cucullata* (= *M. abietis*), *M. gracilis* and *M. muscicola* in the genus. As already discussed, *M. irregularis* and *M. vitellina* are placed in the genus *Spragueola* in this study.

In *Mitrula* the central tissue of the stipe and head consists of loosely interwoven hyphae, which in the older ascocarps may disappear leaving the ascocarp hollow. The outer hyphae of the stipe are compact and parallel. They continue into the head, forming a compact somewhat interwoven layer beneath the hymenium. The hymenium covers most or all of the head and ends abruptly at the stipe in *M. paludosa* (Fig. 11) and *M. morchelloides*. In *M. gracilis* there is some variation. In some ascocarps the stipe gradually widens above, forming a sterile area on the lower portion of the head. In *M. abietis* there is a narrow sterile zone between the stipe and the more or less incurved margin of the hymenium (Fig. 15). According to Corner (1930) this is due to a limited marginal growth of the hymenium producing a narrow collar which is sterile below. This is a development which is more pronounced in the Cudonieae resulting in the pileate ascocarp. Corner has noted a very slight marginal growth of the hymenium in *Microglossum viride* and the tendency may occur in other species of the Geoglosseae. The ascospores of *Mitrula* are somewhat similar in shape to those of *Microglossum* but are much smaller.

According to the studies of Dittrich (1902) and Durand the very young ascocarp of *M. paludosa* is covered with a slight membrane which disappears very early in its development. Corner (1930) has reported a gymnocarpic development for *M. pusilla* (= *M. abietis*?). The de-

velopments of the other species have not been studied. Imai has separated *M. abietis* and *M. gracilis* and placed them in a genus *Gymnomitrula*.

KEY TO SPECIES OF MITRULA

1. Head yellow to light orange, smooth; stipe white; asci (80-)100-125(-150) \times 5-9 μ ; ascospores 10-17(-20) \times 2-3(-4.5) μ ; on decaying leaves in very wet soil or in water.....*M. paludosa*
1. Head light brown to pinkish buff, smooth; stipe light to dark brown; asci 50-70 \times 4-6 μ ; ascospores 10-14 \times 2-2.5 μ ; on decaying needles of conifers.....*M. abietis*
1. Head ochraceous to orange buff, rugose, cerebriform or sometimes smooth; stipe lighter than head; asci 60-90 \times 6-9 μ ; ascospores 9-12(-14) \times 1.5-2 μ ; on mosses.....*M. gracilis*
1. Head pale brown, irregularly longitudinally furrowed; stipe concolorous; asci 36-50 \times 4-6 μ ; ascospores 5-7 \times 2-2.5 μ ; on wet soil.....*M. morchelloides*

MITRULA PALUDOSA Fr., Syst. Myc. 1: 491. 1821. (Figs. 10, 41, 42)

Ascocarps scattered to crowded, subcapitate, 1-4 cm long; ascogenous portion obovoid, cylindric or subglobose, 3-12 \times 2-10 mm, cream-yellow, capucine-yellow, light ochraceous or light orange, drying light ochraceous salmon to brownish orange; stipes terete, 1-2 mm thick, satiny white, translucent, somewhat viscid to glutinous, drying light brownish orange; asci clavate, (80-)100-125(-150) \times 5-9 μ , + I; ascospores clavate, subcylindric, subfusoid or cymbiform, 10-17(-20) \times 2-3(-4.5) μ , 1-celled or rarely 1-septate; paraphyses filiform, branched below, straight, slightly enlarged above.

On decaying leaves on very wet soil, in pools, swamps or *Sphagnum* bogs. Collected in Michigan from June 8 to July 20.

Specimens studied: 70 from Connecticut (CUP), Delaware (CUP), Maine (MICH, CUP), Massachusetts (CUP), Michigan (MICH), Mississippi (MICH), Montana (MICH), New Hampshire (CUP), Ohio (MICH), Pennsylvania (MICH, CUP), Tennessee (MICH), Vermont (CUP), West Virginia (MICH, CUP), British Columbia (CUP), Nova Scotia (CUP), Ontario (CUP).

This species is treated by Durand as *Mitrula phalloides* (Bull.) Chev. It is a common species in the northern hemisphere in cold wet places, pools, bogs, *Sphagnum* swamps in late spring and early summer. When fresh, the viscid to glutinous ascocarps with yellow to light orange heads and white satiny stipes are very distinctive. The upper part of the ascocarp is enlarged into a head which is completely covered by the hymenium.

Three types of ascospores occur in the collections which are here included in this species. The most common type has narrowly clavate, straight spores rounded at both ends (FIG. 42). A few collections have narrowly fusoid, cymbiform or sublunate, straight or somewhat curved, spores with acute ends (FIG. 41). Some collections have broader, oblong, obovoid or subfusoid, straight spores with rounded ends.

MITRULA ABIETIS Fr., Syst. Myc. 1: 492. 1821. (FIGS. 13, 14, 15, 43, 44)

Geoglossum cucullatum Fr., Elench. Fung. 1: 233. 1838.

Mitrula cucullata Fr., Epicr. Myc. 584. 1838.

Heyderia cucullata Boud., Bull. Soc. Myc. Fr. 1: 110. 1885.

Gymnomitrula abietis Imai, Jour. Faculty Agr. Hokkaido Imp. Univ. 45: 173. 1941.

Ascocarps scattered, capitate, 3–20 mm long; heads cylindric to hemispheric, 1–7 × 0.5–2 mm, light brown to pinkish buff, sharply distinct from the stipe; stipes very slender, terete, 0.2–0.7 mm thick, light to dark brown, slightly pruinose above, often with a brown tomentum below; asci clavate, 50–70 × 4–6 μ , ascospores fusoid, subfalcate or narrowly cymbiform, 10–14 × 2–2.5 μ , acuminate at both ends or acuminate at one end and rounded at the other, straight or slightly curved, one-celled; paraphyses slender, clavate, hyaline, branched below.

On fallen needles of conifers (spruce, hemlock, fir and larch).

Specimens studied: 42 from California (MICH), Colorado (MICH, CUP), Idaho (MICH), Michigan (MICH), Montana (MICH), New Hampshire (CUP), New York (MICH, CUP), Oregon (MICH), Washington (MICH), Ontario (MICH).

This species was treated by Durand as *M. cucullata* (Batsch) Fr. It is a very small, inconspicuous species occurring on the fallen needles of conifers and is widely distributed in the northern hemisphere. *M. pusilla* Fr., on pine needles, is considered by Nannfeldt (1942) to be the same species.

MITRULA GRACILIS Karsten, Hedwigia 22: 17. 1883. (FIGS. 12, 45)

Mitrula muscicola E. Henn., Ofvers. Kongl. Vet. Akad. Förel. 42: 71. 1885.

Gymnomitrula gracilis Imai, Jour. Faculty Agr. Hokkaido Imp. Univ. 45: 175. 1941.

Type: In Herb. Bot. Mus. Univ. Helsingfors according to Durand.

Ascocarps capitate, 1-3 cm long; heads very variable, irregularly globoid, obovoid, ovoid, ellipsoid, reniform, occasionally flattened, $2-6 \times 1.5-7$ mm, rugose, convoluted or cerebriform or nearly smooth, pale ochraceous, light orange-yellow, salmon- or orange-buff, covered by the hymenium; stipes terete, 1 mm thick, creamy white or somewhat lighter than the head, smooth; asci clavate, $60-90 \times 6-9 \mu$; ascospores fusoid or fusoid-cylindric, $9-12(-14) \times 1.5-2 \mu$, straight or curved, acute or somewhat rounded at the ends, one-celled or rarely 1-septate; paraphyses filiform, slightly thickened above, as long as the asci.

Growing amid mosses and probably parasitic on them. It has been found in association with *Paludella squarrosa*, *Webera nutans* and *Aulacomnium palustre*.

Specimens studied: Colorado, C. H. Kauffman, August 1917, September 1920 (MICH); Seaver and Bethel, September 1910 (NY); Idaho, A. H. Smith 45901, 45983 (MICH); Montana, E. B. Mains 6117 (MICH); Washington, A. H. Smith 30046, 40591, 40602, 48875 (MICH); Labrador, A. C. Waghorne (CUP); Newfoundland, A. C. Waghorne (CUP).

This species has been rarely found in North America. In addition to the collections cited it has also been reported from Labrador, Newfoundland and Greenland. It apparently is an alpine and arctic species and is rarely collected. It is closely related to *M. paludosa*, differing in the rugose head, smaller asci, colored stipes and close association with various mosses.

MITRULA MORCHELLOIDES Mains, Mich. Acad. Sci. Arts, Letters 20: 83. 1935. (FIG. 46)

Ascocarps capitate, slender, 18-20 mm long; heads cylindric to ellipsoid, $1-2 \times 1$ mm, more or less irregularly longitudinally furrowed, pale brown; stipes filiform, concolorous; asci clavate, $36-50 \times 4-6 \mu$; ascospores fusoid-ellipsoid, $5-7 \times 2-2.5 \mu$, slightly curved; paraphyses filiform.

In wet soil, Wagner's Falls, Munising, Michigan. June 12, 1933, E. B. Mains 33-193. Type (MICH).

This species is known only from the type specimen. The small, slender ascocarps with longitudinally ridged heads and small ascospores distinguish it from other species of the genus.

VERPATINIA Whetzel & Drayton, Mycologia 37: 690. 1945

Ascocarps capitate, stipitate, fleshy, ashy gray, clay colored or brown, arising from sclerotia; head campanulate, cylindric or turbinate, sharply

delimited from the stipe, wrinkled with more or less longitudinal furrows; stipe slender, terete, 0.5 mm thick; asci clavate, + I; ascospores fusoid, cymbiform, allantoid or somewhat lunate, one-celled, hyaline; paraphyses linear or narrowly clavate; sclerotia elongated, black, developing in and mostly digesting elements of leaf, covered with a well-differentiated rind.

Type: *Verpatinia calthicola* Whetzel.

Several species of *Mitrula* (*M. sclerotiorum* Rostrup, *M. brassicae* Hamm. and *M. sclerotipus* Boud.) have been described with sclerotia from Europe and one (*M. shiraiana* (Henn.) Ito & Imai) from Asia. Imai (1941) has proposed a genus *Scleromitula* with *M. shiraiana* as the type. He separates it from *Mitrula* on account of occurrence of sclerotia and a conidial stage. He also has included *M. sclerotiorum* and *M. sclerotipus*. Recently Røed (1945) has concluded that *M. sclerotiorum* does not produce sclerotia but is parasitic on the sclerotia of *Sclerotinia trifoliorum*. *Mitrula shiraiana* occurs on the fruits of the mulberry in Japan. There is also a *Sclerotinia* (*S. shiraiana*) on mulberry fruits in Japan. This is a suggestive parallelism.

These species are unknown for North America. However, Whetzel (1945) has proposed a genus *Verpatinia* for two species which produce ascocarps similar to *Mitrula* from sclerotia. Whetzel (1945) has included *Verpatinia* in the Sclerotiniaceae. In establishing the family he states that the ascocarp is typically cupulate except in one genus (*Verpatinia*) where it is verpoid. Whetzel cultured both species and obtained sclerotia on nutrient agar. A conidial stage was not obtained. The development, ascocarps and ascospores appear similar to *Mitrula*, especially *M. abietis*. Whether *Scleromitula* and *Verpatinia* are congeneric is questionable. The uncertainty of the status of *Scleromitula* makes it undesirable to unite the two at this time.

VERPATINIA CALTHICOLA Whetzel, Mycologia 37: 692. 1945. (FIG. 47)

Type: Labrador Lake, New York, H. H. Whetzel (CUP 25926).

Ascocarps capitate, 7-20 mm long; heads campanulate, subcylindric or turbinate, 2-3 × 1-2 mm, clay color to Sayal brown, rugose with irregular pits or furrows, often longitudinally ridged; stipe terete, 0.5 mm thick, smooth, somewhat lighter colored than the head; asci clavate, 30-50 × 4-6 μ ; ascospores subfusoid, narrowly cymbiform or somewhat allantoid, 6-8(-10) × 2-2.5 μ , one-celled; paraphyses linear to narrowly clavate, straight; sclerotia narrow, ovate or oblong, tapering to pointed

ends, 3-10 × 1 mm, black, the upper exposed surface convex, longitudinally striate.

On decaying petioles of *Caltha palustris*.

Specimens studied: New York, H. H. Whetzel, CUP 21996, CUP 25926 type; Ontario, J. W. Groves & J. L. Conners, CUP 26449.

Collections 21996 and 25926 produced sclerotia in decaying petioles of *Caltha palustris*. The substratum for number 26449 is uncertain. The species was cultured by Whetzel on potato dextrose agar. It is stated that it formed a felty gray aerial mycelium bearing small black, much-fluted, irregular anastomosing sclerotia. The dried specimen of such a culture has pulvinate sclerotia approximately 1-mm in diameter.

VERPATINIA DUCHESNAYENSIS Whetzel, *Mycologia* 37: 694. 1945

Type: On leaves of *Betula lutea*, Duchesnay, County Portneuf, Quebec, H. H. Whetzel, CUP 28011.

Ascocarps capitate; heads cylindric or turbinate, 2 × 1 mm, ashy gray, deeply and irregularly wrinkled; stipe slender, terete, 0.5 mm, brownish, smooth, fibrillose at the base; asci clavate, 66-75 × 6 μ; ascospores fusoid, narrowly cymbiform or somewhat lunate, 6-12 × 2.5-3 μ; paraphyses clavate; sclerotia elongate in the veins, up to 25 mm long, black.

This species is known only from the type specimen. Only a few ascocarps were collected. The species was cultured by Whetzel on potato dextrose agar, growing slowly and forming chocolate brown to black, much-convoluted sclerotial masses several centimeters in diameter. On account of the limited amount of material available for study the above description has been mostly taken from that published by Whetzel. The species appears to have larger asci and more fusoid ascospores than *V. calthicola*. In culture the large convoluted sclerotial masses are distinctive.

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OBSERVATIONS ON GYMNOASCACEAE. II. TWO NEW SPECIES OF MYXOTRICHUM

HAROLD H. KUEHN

(WITH 61 FIGURES)

The purpose of the present paper is to present descriptions of two more new species of *Myxotrichum*, to illustrate their developmental morphology, and to discuss gametangial relationship among species of *Myxotrichum*, as far as they are known at the present time. In the first paper of this series (Kuehn, 1955) the writer has provided a detailed description of *Myxotrichum uncinatum* and has presented a description of a new species, *Myxotrichum emmonsii*. This first paper, however, was concerned only with the developmental morphology of the species discussed.

Literature concerning the work previously reported on the developmental morphology of species of *Myxotrichum* has been reviewed in the first of these two papers. The methods employed in the present study are the same as those described in that paper. The organisms were grown on various media in Petri dishes. Minute tufts of hyphae were removed and slides were prepared for examination with the microscope. For later stages, the peridium of the immature ascocarp was removed under a dissecting microscope. By pressure on the cover slip the contents of the ascocarp were spread out on a slide making the croziers evident.

OBSERVATIONS AND DESCRIPTIONS OF SPECIES

Myxotrichum thaxteri sp. nov.¹

Cleistothecii globosis, 214-479 μ diam. appendiculis exclusis, pallide-brunneis vel brunneis. Peridii hyphis pallide brunneis, septatis, asperulatis, 4.2-5.6 μ diam. Appendiculis biformibus: vel brevibus, asperulatis spinis, 2.9-3.0 \times 7.0-32.2 μ , vel longis aseptatis appendiculis omnibus ad apicem uncinatis, apicibus plerumque perfecte circinatis, levibus, ad basim asperatis, 2.7-3.3 \times 252-542 μ . Ascis hyalinis, ellipticis vel obovatis, 5.0-5.6 \times 6.8-7.2 μ , octosporis. Ascosporis hyalinis, echinu-

¹ The writer acknowledges with appreciation the assistance of Dr. D. P. Rogers, New York Botanical Garden, for the preparation of the Latin diagnoses.

latis, globosis, 2.8–2.9 μ diam., vel ovoideis, 2.6–2.7 \times 2.7–2.8 μ . Hyphis sterilibus hyalinis, 1.2–1.6 μ diam. Oidiis hyalinis, 1.4–1.6 \times 2.8–7.2 μ .

Cleistothecia spherical, light brown to brown in culture, light yellow-brown under the microscope, 214–479 μ in diameter, not including the appendages. The peridium is composed of light yellow, septate, cuticularized, asperulate hyphae, 4.2–5.6 μ in diameter. Appendages are of two types: short, asperulate spines, 2.9–3.0 \times 7.0–32.2 μ , and long non-septate appendages, all of which are hooked at the apex and with most of the tips completely inrolled, smooth except near the base where they are asperulate, 2.7–3.3 \times 252–542 μ . Asci hyaline, elliptical to obovate, 5.0–5.6 \times 6.8–7.2 μ , eight-spored. Ascus wall ephemeral, the spores adhering in a ball 6.9–7.3 μ in diameter. Ascospores hyaline, echinulate, spherical and 2.8–2.9 μ in diameter, or ovoid and 2.6–2.7 \times 2.7–2.8 μ . Vegetative hyphae hyaline, 1.2–1.6 μ in diameter, not including the racquet mycelium present. The imperfect phase is represented by hyaline oidia, 1.4–1.6 \times 2.8–7.2 μ .

Colonies on Sabouraud's dextrose agar are slow growing, white from the start, with small brownish areas appearing with age. Reverse of the colony is colorless or tinged with yellow. Ascocarps, of which few are formed, appear at first as white tufts of hyphae toward the periphery of the colony. Mature cleistothecia are brown and usually are present within 23 days, although in some cultures they do not appear for as long as 3 months after the plates are inoculated.

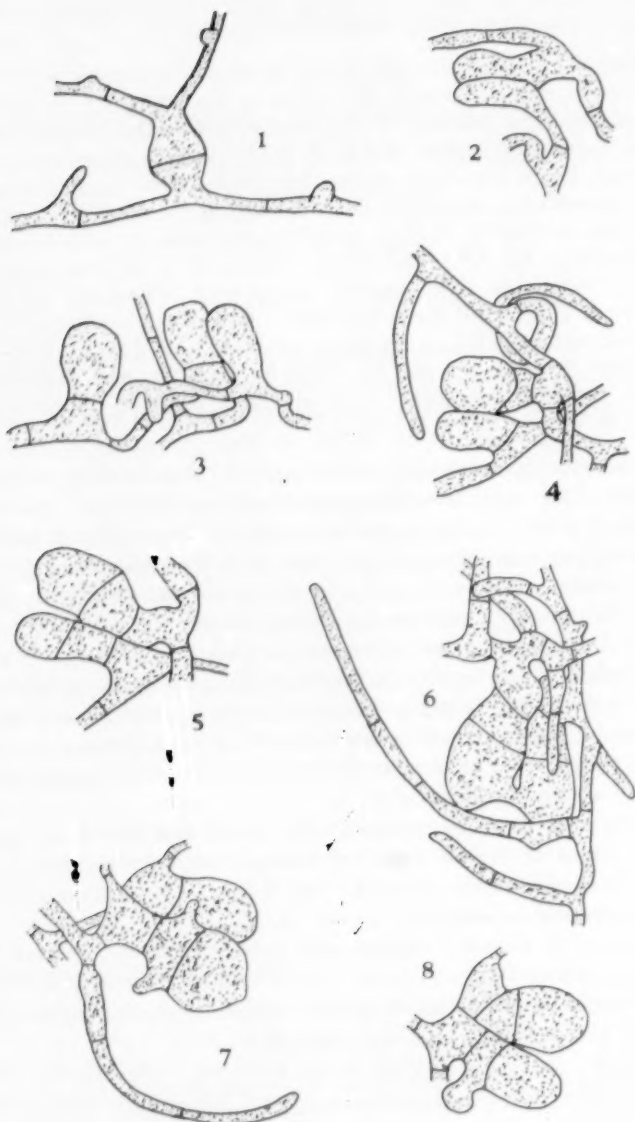
Colonies on Sabouraud's maltose agar resemble those on Sabouraud's dextrose agar. On Sabouraud's maltose agar, however, cleistothecia are abundantly formed and are more uniformly present throughout the colony, although they occur more frequently toward the periphery, where they are usually in clusters.

Colonies on PDA grow rapidly, and are at first flocculent, but later brown crusts of hyphae form below the overlying flocculent hyphae. Cleistothecia are rarely produced, but if they are, they are of normal dimensions and appearance.

Colonies on Czapek's solution agar grow very slowly, and are sparse in appearance and white in color. The reverse of the colony is colorless. Cleistothecia are produced abundantly within 15 days as white tufts of hyphae, and become brown with maturity.

Colonies on Yp.Ss. agar are white, flocculent. The reverse is tinged yellow. Within 20 days ascocarps appear abundantly throughout the colony. For ascocarp production, this medium was found to be best of those utilized.

This species was isolated by Roland Thaxter from *Solenodon* (opos-

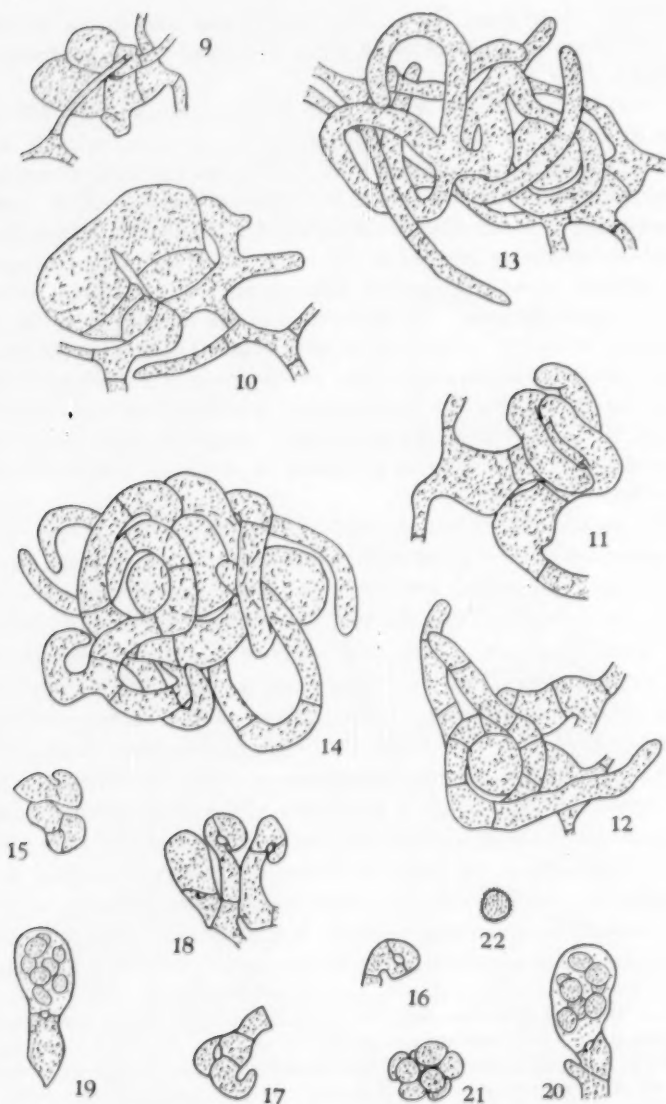
FIGS. 1-8. *Myxotrichum thaxteri*.

sum-shrew) dung from Haiti. The fungus was sent to the Northern Regional Research Laboratory in June, 1940, and it is now designated as NRRL 1714.

Myxotrichum thaxteri differs from *M. emmonsii* and the following newly described species, *M. conjugatum*, the two species with which it is most closely allied, as follows: 1. *M. thaxteri* has hyaline vegetative hyphae while the other two species have orange hyphae. 2. *M. thaxteri* has appendages which may be straight but usually are either simply hooked or completely inrolled at the apex, while the other two species have straight appendages which only occasionally or rarely may be slightly bent at the apex. 3. The reverse of the colonies in *M. thaxteri* is colorless to slightly yellow, while in the other two species the reverse of the colonies is red-orange. The development of a trichogyne from one of the gametangia is a characteristic which can be utilized to distinguish *M. thaxteri* from any of the other species of *Myxotrichum* thus far investigated. The species is named in honor of Roland Thaxter, who isolated this fungus.

The gametangial initials formed in this species are unique in the Gymnoascaceae. The gametangia usually are formed in pairs, but instances are encountered frequently in which non-functional solitary initials are formed. Typically two morphologically similar, club-like short, lateral branches, usually from different hyphae, are formed adjacent to one another (FIG. 2). Two septa are deposited in each parent hypha, one on each side of a gametangium, so that each gametangium appears to have "two legs" (FIG. 3). Each gametangium becomes once or twice septate, with the two gametangia of a pair not necessarily similarly septate (FIGS. 4, 5). A projection arises from the apical cell of one initial to establish contact with the apical cell of the other (FIGS. 5, 6). The walls at the point of contact break down, resulting in the formation of a fertilization tube, which could be designated as a trichogyne, between the copulating initials. Ascogenous hyphae are produced from either the terminal cell of one of the organs (FIG. 11), or from the

FIGS. 1-8. *Myxotrichum thaxteri*. 1. A pair of very young gametangia as seen from above. 2. Young gametangia, lateral view. 3. A solitary gametangium adjacent to a pair of gametangia. 4. One gametangium has become twice septate, while the other gametangium is once septate. 5. Both gametangia are twice septate. From the apical cell of one gametangium there appears a bulge which will develop into the trichogyne. 6. The cell walls have dissolved at the point of contact of the trichogyne. 7. Branches appear from the subterminal cell of one of the gametangia. 8. One branch is produced from the subterminal cell of one of the gametangia, all $\times 1300$.



FIGS. 9-22. *Myxotrichum thaxteri*. 9. A branch appearing from the sub-terminal cell of one of the gametangia. The gametangia are not equally septate. 10. Stage at which dissolution of the cell walls occurs. 11. A branch, which has arisen from the terminal cell of one of the gametangia, is encircling the other

subterminal cell (Figs. 7, 8). It has not been possible to ascertain whether or not the ascogenous hyphae arise only from that gametangium which produces the trichogyne. Aceto-carmin preparations were prepared in unsuccessful efforts to elucidate the nuclear cytology.

The ascogenous hyphae coil about the initials to form a dense clump (Figs. 12-14). Septa divide the ascogenous hyphae into several cells (Fig. 12) from which croziers are produced. The penultimate cell as well as the cell formed by the fusion of the antepenultimate and ultimate cells produces hyphae which recurve to form additional croziers. Eventually, the penultimate cells of croziers become asci.

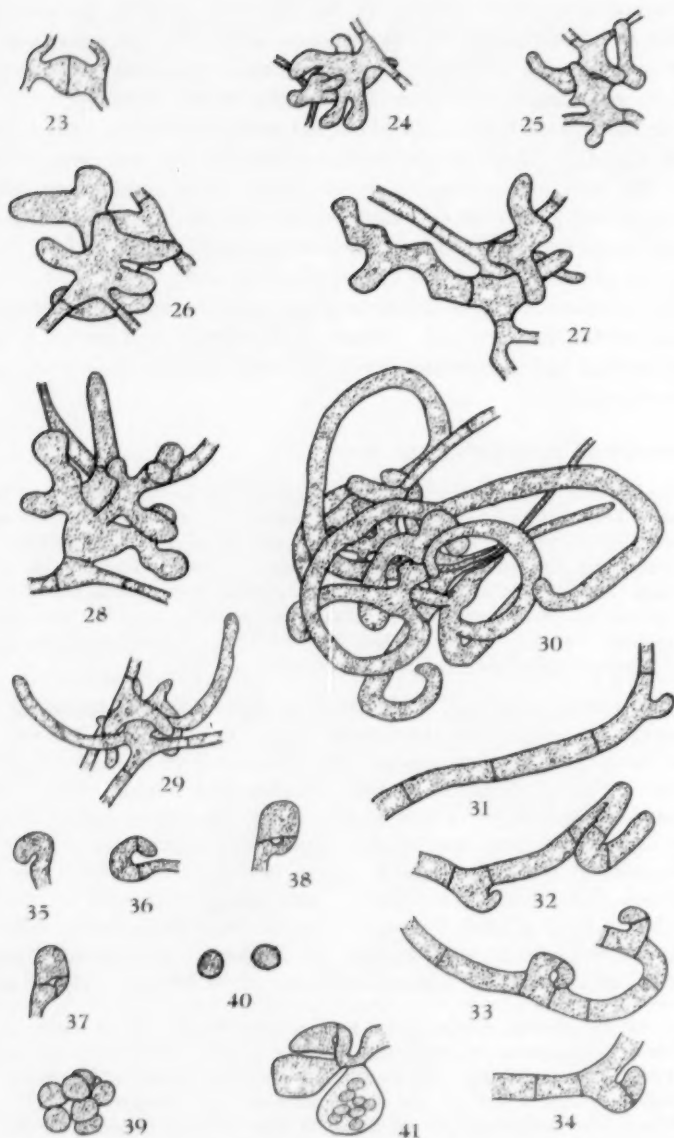
The peridium arises by thickening and cuticularization of vegetative hyphae surrounding the coil. Many of the cleistothecia are of a compound nature, and contain asci which had their origin from several pairs of gametangia.

***Myxotrichum conjugatum* sp. nov.**

Cleistothecii globosis, 252-504 μ diam. appendiculis exclusis, pallide ad atro-brunneis. Peridii hyphis pallide brunneis, asperulatis, septatis, 2.6-3.0 μ diam. Appendiculis bifimbriatis: vel brevibus, asperulatis spinis 1.4-2.8 \times 7.0-28.0 μ , vel longis, aseptatis appendiculis ad apicem uncinatis vel non, levibus, prope basim asperulatis, 2.8-3.2 \times 226-731 μ . Asci hyalini, elliptici vel obovati, 4.2-5.0 \times 6.8-7.1 μ , octospori. Ascospores hyalini, globosi vel ovoidei, superficie tota echinulata, globosis 2.8-3.1 μ diam., ovoideis 2.6 \times 2.9-3.2 μ . Hyphis sterilibus luteis, 1.2-1.5 μ diam. Oidiis hyalinis, 1.2-1.5 \times 4.0-4.4 μ .

Cleistothecia spherical, 252-504 μ in diameter, not including appendages. In culture the ascocarps appear light to dark brown, but under the microscope they appear light yellow to light brown. Peridium of light yellow, asperulate, septate, cuticularized hyphae, 2.6-3.0 μ in diameter. Appendages of two types: short, asperulate spines, 1.4-2.8 \times 7.0-28.0 μ , and long, non-septate appendages which may or may not be uncinatate at the apex, smooth except near the base where they are asperulate, 2.8-3.2 \times 226.8-731.0 μ . Asci hyaline, elliptical to obovate, 4.2-5.0 \times 6.8-7.1 μ , and 8-spored. Ascus wall ephemeral, with the spores adhering in a ball 5.6-7.0 μ in diameter. Ascospores hyaline, spherical or ovoid, with fine echinulations often detected only at about

initial. 12. Ascogenous hyphae which have become septate. 13. A rather extensive clump of ascogenous hyphae which have not yet become septate. 14. Septate, branched ascogenous hyphae. 15. Croziers in the initial stages of formation. 16. A crozier showing fusion of the antepenultimate and ultimate cells. 17. The penultimate cell elongating and recurving to form another crozier. 18. An immature ascus and two croziers at the apex of ascogenous hyphae. 19-20. Asci with ascospores. 21. Ball of ascospores following the dissolution of the ascus wall. 22. A mature ascospore, all \times 1300.

FIGS. 23-41. *Myxotrichum conjugatum*.

$\times 1800$; spherical spores $2.8-3.1 \mu$ in diameter; ovoid spores $2.6 \times 2.9-3.2 \mu$. Vegetative hyphae orange, $1.2-1.5 \mu$ in diameter, not including the racquet mycelium which is also present. The imperfect spore phase is represented by hyaline oidia with dimensions of $1.2-1.5 \times 4.0-4.4 \mu$.

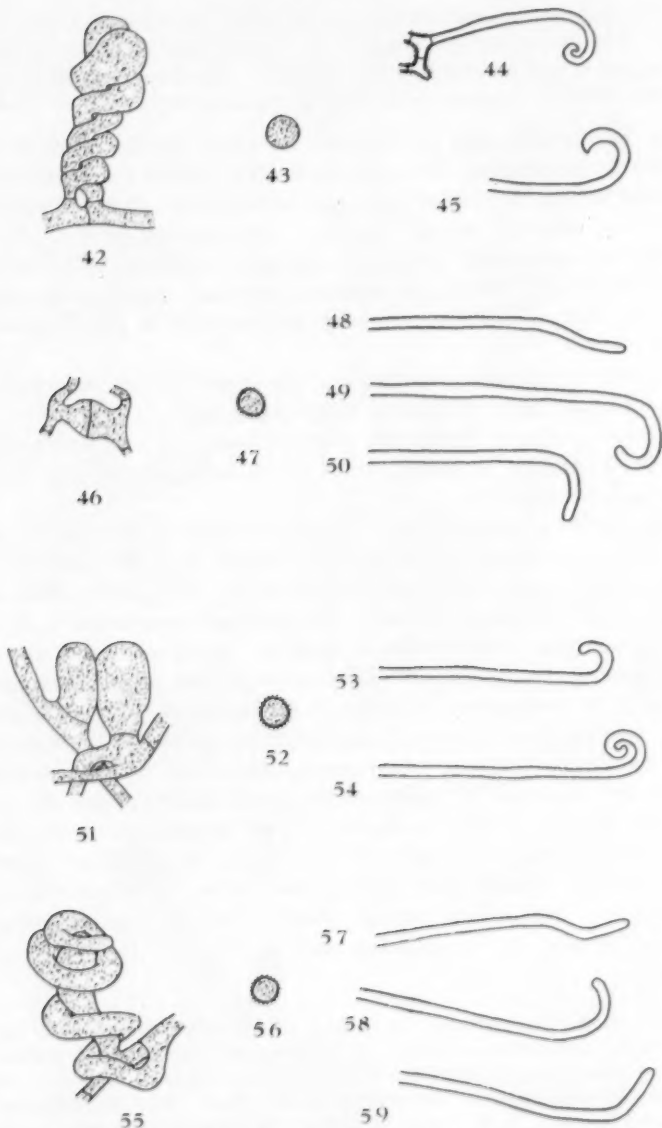
On Sabouraud's agar the colonies are white and flocculent at first, but later become orange. Overgrowth of white hyphae frequently occurs in limited areas. Reverse of the colony is red-orange from the start, the pigment not diffusing into the medium. Ascocarps appear in 2-3 weeks as white tufts of hyphae scattered in the aerial mycelium or on the surface of the colony. Mature cleistothecia, with asci, are found after about 25 days. They are brown, spherical, and scattered uniformly over the colony.

Colonies on Czapek's solution agar are restricted, but otherwise are similar in appearance to those on Sabouraud's agar.

Emmons isolated this species from Arizona soil. It was obtained from Dr. Hesseltine as NRRL 1244. It is designated also as #47 of Emmons' collection.

The species is characterized by having a light to dark brown ascocarp with appendages which may be straight or simply curved terminally, and by possessing spherical, echinulate ascospores. It is most similar to *M. emmonsii* Kuehn. The spherical ascospores in *M. emmonsii* are slightly smaller than those in *M. conjugatum*, and, also, the appendages of the ascocarp do not become as long in *M. emmonsii* as they do in *M. conjugatum*. The structure and appearance of the gametangia constitute an important distinguishing characteristic separating these two species. *Myxotrichum conjugatum* differs from *M. johnstoni* Massee & Salmon and *M. spinosum* Massee & Salmon in that *M. spinosum* has ellipsoid, smooth ascospores and the appendages on the brown ascocarp are always absolutely straight, while *M. johnstoni* possesses spores that are smooth and elliptical, and it has ascocarps which are yellow-green (Massee and Salmon, 1902). The distinguishing characteristics between *M. conjugatum* and *M. thaxteri* have been cited already.

FIGS. 23-41. *Myxotrichum conjugatum*. 23. Morphologically similar gametangia arising from adjacent hyphae. 24-29. Branches arise from both initials, but those from one organ (designated as the ascogonium) elongate to a greater extent, while the branches from the antheridium remain short. 30. Coil surrounded by ascogenous hyphae. 31-34. Stages in crozier formation from septate ascogonial hyphae. 35-38. Stages in crozier formation. 38. Shows the fusion of ultimate and antepenultimate cells. 39. Clump of spores left after disappearance of the ascus wall. 40. Mature ascospores. 41. Distal end of ascogenous hypha showing mature ascus and stages in its development, all $\times 1300$.



FIGS. 42-59. Comparison of gametangial relationships, spore characteristics, and tips of appendages in certain species of *Myxotrichum*. 42-45. *Myxotrichum uncinatum*. 42. Coiling gametangia, $\times 1300$. 43. Ascospore, $\times 1300$. 44, 45. Two

The initials found in this species are of a type not found elsewhere in the Gymnoascaceae as far as is known at the present time. Morphologically similar, club-like projections are put forth from two adjacent hyphae. The projections, which are the young gametangia, meet and become flattened against one another terminally (FIG. 23). Both may become separated from their parent hypha by septa. However, often an initial is not delimited at this point from the cell of the parent hypha which gave rise to it. Branches, which are not constant in diameter and are irregular in shape, arise from both of the gametangia (FIGS. 24-29). Although no examples were found which provided conclusive evidence, it is probable that only those branches of one gametangium, the functional ascogonium, elongate. Indication that this is what occurs may be seen in FIGS. 27 and 29. The numerous elongating ascogenous hyphae from the ascogonium coil loosely and irregularly about the gametangia (FIG. 30) and often extend for some distance into the surrounding vegetative hyphae. Septa divide the ascogenous hyphae into many cells, several of which produce croziers laterally (FIGS. 31-34). Some penultimate cells may produce asci directly, others continue growth as ascogenous hyphae. Asci are eventually formed from the penultimate cells of croziers (FIG. 41).

The peridial hyphae are formed from surrounding vegetative hyphae, which increase in diameter, and then this is followed by a cuticularization of their walls. They become asperulate and yellow. Compound ascarps are found frequently.

DISCUSSION

Myxotrichum thus far has been the most thoroughly investigated genus of the Gymnoascaceae, and a variety of gametangial types have been found that characterize the different species in this genus. From a comparison of the four species of *Myxotrichum* which have been investigated by the author it can be seen that gametangial morphology will prove useful for taxonomical purposes. *Myxotrichum uncinatum*, as interpreted here (Kuehn, 1955), can be distinguished from the other three species by the nature of its appendages, which are short and hooked

appendages, one only partially shown, $\times 263$. 46-50. *Myxotrichum conjugatum*. 46. Gametangia, $\times 1300$. 47. Ascospore, $\times 1300$. 48-50. Three appendages, with only the terminal portion shown, $\times 263$. 51-54. *Myxotrichum thaxteri*. 51. Gametangia prior to formation of the trichogyne, $\times 1300$. 52. Ascospore, $\times 1300$. 53, 54. Two appendages, each with only the terminal portion shown, $\times 263$. 55-59. *Myxotrichum emmonsii*. 55. Coiling gametangia, $\times 1300$. 56. Ascospore, $\times 1300$. 57-59. Three appendages showing only the terminal portion of each, $\times 263$.

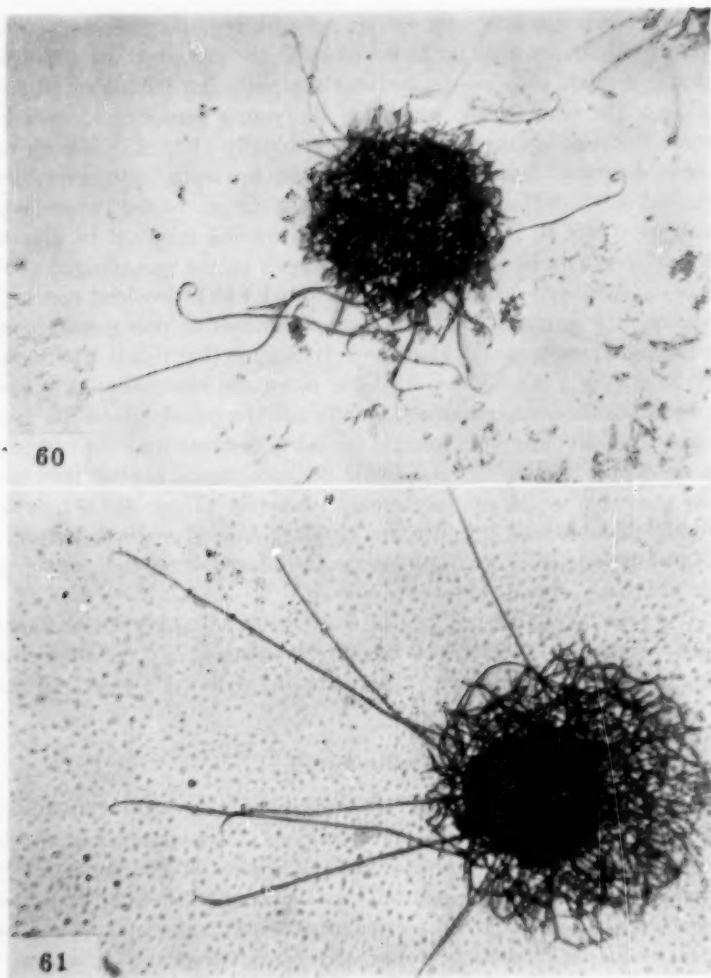


FIG. 60. Cleistothecium of *Myxotrichum thaxteri*. $\times 91$.

FIG. 61. Cleistothecium of *Myxotrichum conjugatum*. $\times 123$.

at the apex (Figs. 44, 45). The isolate of *M. uncinatum* studied (Kuehn, 1955) possesses smooth ascospores. Massee and Salmon (1901) reported the spores for this species to be minutely asperous. Saccardo (1889), Eidam (1880), and Schroeter (1893) did not state whether the spores in this species were smooth or asperulate.

The other three species which were investigated by the author, *M. conjugatum*, *M. thaxteri*, and *M. emmonsii*, all have asperulate ascospores. Moreover, *M. conjugatum* and *M. emmonsii* have similar appendages in that they rarely are hooked, and usually are straight or only slightly curved terminally (Figs. 48-50; 57-59). However, these latter two species possess gametangia of such extremely different types that they can be distinguished easily when young stages in ascocarp formation are examined. In *M. conjugatum* (Fig. 46) the gametangia are formed as short, lateral branches of adjacent hyphae. The branches come into contact and become flattened against one another at their apices, resembling the progametangial stage of certain Mucorales. In *M. emmonsii* the central, straight antheridium becomes encircled by the more slender coiled ascogonium (Fig. 55).

Myxotrichum thaxteri possesses appendages all of which are uncinata to a certain extent, with some completely inrolled as in *M. uncinatum* (Figs. 53-54). However, it is possible that certain strains of this species might produce so few appendages which are completely inrolled at the apex that such might be overlooked. An examination of the gametangia in these cultures would facilitate the identification of this species immediately, since *M. thaxteri* is the only species known at the present time in which a trichogyne develops between the gametangia (Fig. 51). In this species the two short, clavate gametangia at first are contiguous laterally as well as toward the apical region. A projection, the trichogyne, appears from the apex of one gametangium and forces the two apices apart, following which a dissolution of the cell walls takes place and plasmogamy is accomplished.

SUMMARY

1. Diagnostic characteristics are provided for two new species, *Myxotrichum thaxteri* and *M. conjugatum*.
2. The morphological development of these two species is discussed and illustrated. The formation of ascogenous hyphae and croziers precedes the production of asci.
3. A comparison is made of the gametangial types represented in *Myxotrichum uncinatum*, *M. thaxteri*, *M. emmonsii*, and *M. conjugatum*. The value of gametangial morphology in taxonomy is discussed.

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THE GENUS MYLITTOPSIS

DONALD P. ROGERS AND G. W. MARTIN

(WITH 6 FIGURES)

Sixty years ago Patouillard published a lucid and detailed description, and five years later clear illustrations, of a fungus which he assigned to a new genus *Myliopsis*, a cartilaginous, nodular or cerebriform member of the Auriculariaceae. Since that time, partly from the rarity of the fungus, and partly from uninhibited misinterpretation of the description, the genus has become and remained unknown in the literature and to mycologists. The single species, *M. Langloisii*, was represented by a single collection, divided between the herbaria of Ellis and Patouillard. The only later student to discuss *Myliopsis* in print was Höhnelt (Ann. Myc. 15: 293-296. 1917), who examined neither of these specimens, and whose imaginative attempts to equate the fungus to others of which also he had seen no original material resulted in complete confusion. In the United States, an influential contemporary mycologist saw in *Myliopsis* (as his notes show) only the *Ptychogaster* form illustrated in Brefeld's *Untersuchungen* (8: pl. 8, f. 26-33. 1889). The authors of the two standard compilations of genera, Killermann (E. & P. Nat. Pfl. 2 Aufl. 6: 108) and Clements & Shear (Gen. Fung. 341), seem to have been misled by Höhnelt rather than informed by Patouillard; at any rate, they set *Myliopsis* aside as a *genus dubium*.

Examination of the type collection of *Myliopsis Langloisii* shows that Patouillard's interpretation is correct and his characterizations accurate, lacking only a description of the spores, which he did not find, but which are present in his material. Two more recent collections are at hand to confirm the description, and an earlier one, regrettably, as evidence that Patouillard was not the first to name the fungus.

MYLITTOPSIS Pat., Jour. de Bot. 9: 245. 1895; Essai taxon. 15. fig. 9. 1900.

Fructification nodular, cartilaginous, radiate-fibrillose, sometimes with a more fibrous core; basidia linear, 3-septate; spores hyaline, oblong.

Type: *M. Langloisii* Pat.

The fructification has the hymenial structure of *Auricularia*, from which it differs most obviously in form. Of the other genera of the

Auriculariaceae (Martin, Univ. Iowa Studies Nat. Hist. **19** (3): 86. 1952) it resembles only the tuberculiform members of *Platyglea*, such as *P. disciformis* (Fr.) Neuh. (*P. Tiliae* (Bref.) Sacc.; Bourd. & Galz., Hym. Fr. 14. [1928]), differing from typical species in texture, radiate structure, and form. *Mylittopsis* is a monotypic genus, *M. carpinica* (A. & S. ex Fr.) Höhn., Ann. Myc. **15**: 295. 1917 (=*Tremella fragiformis* $\beta\beta$ *carpinica* A. & S., Consp. fung. 301. 1805; *Dacrymyces fragiformis* b. *carpinica* A. & S. ex Fr., Syst. Myc. **2**: 229. 1822) being apparently wholly alien.



FIG. 1. *Mylittopsis marmorata*. Isotype of *M. Langlosii*, NY, $\times 2$.

***Mylittopsis marmorata* (Berk. & Curt.) comb. nov.**

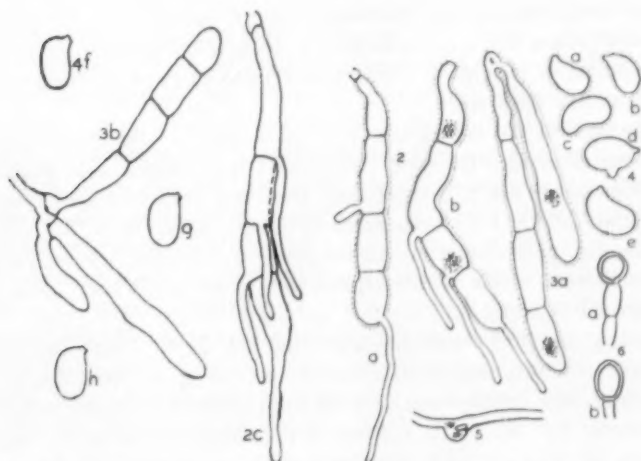
Tremella marmorata Berk. & Curt., Grevillea **2**: 19. 1873. *Mylittopsis Langlosii* Pat., Jour. de Bot. **9**: 247. 1895.

Fructification cerebriform, probably 1–5 cm in diameter, when fresh soft- but dense-cartilaginous, yellowish-brown, when dry very hard, dark brown (Benzo Brown to Aniline Black and Sooty Black (R)), resinous in texture and luster, the surface tuberculate, in section radiate-fibrillose, obscurely concentrically zonate, with occasional internal non-

gelatinous fibrous areas or with a Clay Color (R) fibrous core; hyphae in part with thick walls soon gelatinized and narrow lumina, in part thin-walled and with clamps; basidia linear, transversely 3-septate, subtended by a proliferative clamp, $35-55 \times 3-5 \mu$, each segment at its distal end giving rise to a tubular filament about $1-1.5 \mu$ in diameter; spores oblong-ellipsoid, obliquely apiculate at the base, $6.5-7.5 \times 4-4.5 \mu$.

On oak logs and unidentified wood.

Specimens examined:



FIGS. 2-6. *Mylittopsis marmorata*. Holotype of *M. Langloisii* FH-P. 2. Basidia. 3. Basidial proliferation from basal clamp. 4. Spores. 5. Sterile hyemial element with clamp. 6. Thick-walled bodies—the "conidia" of Patouillard. All $\times 1000$. Granular aggregations in Figs. 2b, 3a and 5 are in position of nuclei; in Figs. 2a, 2b, 3a and 4a-e the solid line indicates the boundary of the lumen and the broken line shows the outer visible limit of the gelatinized wall.

South Carolina: Santee Canal, VIII. 1849, Ravenel 1107, Curtis 3023,

TYPE of *T. marmorata*, FH-C.

Florida: Magnesia Springs, near Gainesville, IX. 3. 54, Cain, TRTC 30899, TRT, NY.

Louisiana: Langlois 2385, TYPE of *M. Langloisii*, NY, FH-E, FH-P.

Malaya: Jahore, Endau R., VII. 1931, R. E. Holttum (comm. Corner 1191), IA, NY.

The dried specimens of this fungus look a good deal more like a very large and excessively convoluted *Daldinia* than like a member of the Tremellales. Langlois reported to Ellis (by whom the fungus was

referred to Patouillard) that his collection was "a dubious excrescence on decaying Polyporus, soft when fresh." The polypore, a very thin form resembling *P. biformis* or *abietinus*, is present in both the New York and the Farlow specimens of the Langlois material, but appears much too tenuous to support such a robust growth as the *Mylittopsis*. It seems certain that the two fungi merely emerged from the wood at the same place, as *Tremella aurantia* and *Stereum hirsutum* have been observed to do in Oregon; and no second fungus is present in the other collections. Langlois further wrote, "2385, found only once in a very swampy wood, was already hardening when collected. . . . Its color was yellowish brown and has darkened by desiccation without losing much of its volume or weight." The cut or broken surfaces of dried material look quite like dark rosin.

The type of *T. marmorata* is a good match. But two additional specimens, filed with the type (Blake 689, from Maine, and Botteri 37, from Mexico, FH-C), are not this; the New Jersey fungus (Sterling, Lloyd coll. 27033, BPI) described in Lloyd, Myc. Writ. 5: 757. fig. 1133, is also quite different. In response to inquiries, several perspicacious collectors of its native region have stated that they have never encountered *Mylittopsis*.

During the 1954 foray at Gainesville Dr. R. F. Cain hunted down an ample fructification of *Mylittopsis*, which, apart from being more effuse and less cerebriform, agrees well with the earlier collections. And finally Dr. E. J. H. Corner sent a neat fructification found by Holtum in Malaya, with somewhat narrower basidia ($3-3.5\ \mu$ rather than mostly $4-4.5\ \mu$ as in the Louisiana specimen) and a well developed fibrous core analogous to that of *Tremella encephala* Pers. (*Naematelia encephala* Fr.). The Malayan collection seems not specifically separable.

Thanks are due to Drs. Cain and Corner; to Dr. D. H. Linder, Dr. Rolf Singer, and Dr. I. Mackenzie Lamb, who have successively permitted examination of material in the Farlow Herbarium; to Mr. John A. Stevenson for the loan of specimens in the National Fungus Collections; and to Mrs. Hertha A. Benjamin for her photograph of the Langlois collection.

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A NEW SPECIES OF CEPHALOSPORIUM¹

S. B. SAKSENA

(WITH 3 FIGURES)

The fungus here described was isolated from a soil sample of a grassland surrounding the Patharia forest near Sagar. It was found during the course of the ecological studies of soil micro-fungi of forests in which the writer has been engaged for the last few years.

GENERAL CHARACTERS. The colony is floccose and pinkish grey at maturity. The conidiophores arise from prominently funiculose structures (FIG. 1, A, B; FIG. 2). The conidia are globose to elliptical, pinkish red and are borne in heads (FIG. 1, A, B; FIGS. 2, 3). The base of the conidia is often flattened (FIG. 1, D).

A search in the available literature did not show any species described with identical characters. The species sharply differs from the others described in its coloration, funiculose habit and the size and shape of the conidia. In view of these differences, the fungus is described as a new species of *Cephalosporium* to be called *Cephalosporium roseo-griseum* after its peculiar coloration.

Cephalosporium roseo-griseum sp. nov.

Coloniae late dispersae in "Czapek agar," atque cito ettingentes diametrum 4-5 cm post 8 dies in temperie normali cubiculi, floccosae, primo albae, cito evadentes roseae in parte aversa vero eiusdem coloris sed paulo altioris; tandem in maturitate color evadit roseo-griseus, in parte aversa vero color evadit altior in differentiis coloris roseo-rubri. Hyphae duplicis naturae: hyphae vegetativae submersae ramosae, repentes, 2.1-2.8 μ crassae; hyphae aerae floccosae, habitum funiculosum frequentius monstrantes, eiusdem densitatis. Mycelium vegetativum monstrat colorationem subrubram, cui totius coloniae color est tributus. Conidiophori lateraliter surgunt ex structuris funiculosis, non ramosi, 35-45 \times 2.1-2.8 μ , non ad apicem tumescentes, supportantes capitulum conidiorum mucro inclusorum; capitula communiter 8-15 μ diam.; conidia ut plurimum ovalia, nonnumquam globosa vel elliptica, monstrantia eundem colorem rubrum vel subrubrum in differentia altiore, sed numquam nigrescentia, dimetientia 5-8 \times 3.5-5.5 μ , parietibus crassis praedita, laevia, altero apice rotundato, altero vero saepe apparenter complanato.

¹ Part of a thesis approved for the degree of Doctor of Philosophy by the University of Saugor.

Colonies on Czapek's agar spreading broadly and rapidly, attaining a diameter of about 4-5 cm in 8 days at room temperature, floccose, white at first but soon becoming pinkish (Color Pl. 11.A 3),² reverse in the same shade but a little deeper (Color Pl. 11.A 5); later at maturity the color turns pinkish grey (Color Pl. 47.A 1) and the reverse

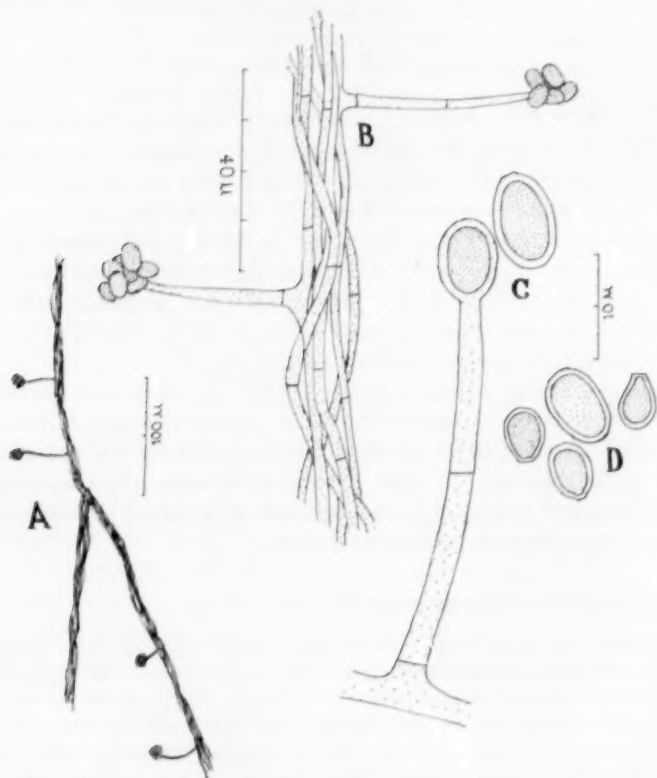


FIG. 1. A. Habit, showing funicular structure and conidiophores, $\times 150$. B. Same, magnified to show terminal balls of conidia, $\times 700$. C. Formation of conidia, $\times 1350$. D. Conidia, showing flattened bases, $\times 1350$.

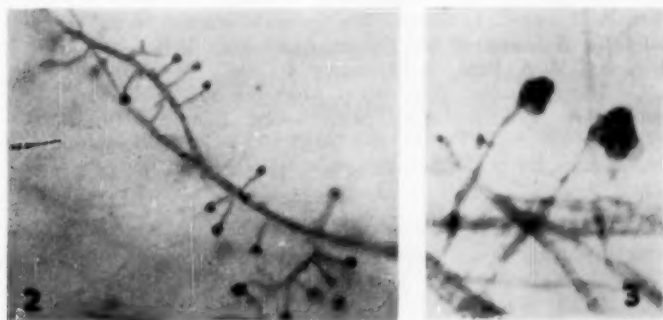
also becomes deeper in the same pinkish red shades. Hyphae of two kinds; submerged vegetative hyphae branched, creeping, $2.1-2.8 \mu$ thick; aerial floccose hyphae showing predominant funiculose habit, of same thickness. The vegetative mycelium shows reddish coloration to which the colony appears to owe the color. Conidiophores arise as side

² The color plates refer to the Maerz & Paul's Dictionary of Color.

braches from the funiculose structures, unbranched, $35-45 \times 2.1-2.8 \mu$, not swollen at the apex, bearing a head of conidia enclosed in slime, heads commonly $8-15 \mu$ in diameter; conidia generally oval, sometimes globose or elliptical, showing the same pinkish red color in deeper shade but never becoming blackish, ranging from $5-8 \times 3.5-5.5 \mu$, thick walled, smooth, with one end round and the other often appearing flattened.

The type culture is being deposited in the Indian type culture collection of fungi, Division of Mycology and Plant Pathology, Indian Agricultural Research Institute, New Delhi.

CULTURAL CHARACTERISTICS. The fungus was tried on several common media in order to note its behavior and range of variability. The growth was faster on malt agar and potato-dextrose-agar, medium on Waksman's agar and slow on soil extract agar. The colonies were



FIGS. 2, 3. 2. Conidiophores developing on predominantly funicular structures, $\times 150$. 3. Conidiophores bearing balls of spores, $\times 650$.

most flocculent on potato-dextrose-agar and least on soil extract agar. The color succession remained almost the same in all cases but the colors were found to be deepest on potato-dextrose-agar and lightest on soil extract agar. The range of measurements remained more or less constant throughout.

SPORE GERMINATION. Germination was tested in pea decoction as well as in Czapek's solution. The spores germinated readily within 8 to 10 hours at room temperature. About 90% of the spores were found to germinate on each slide.

SUMMARY

A new species of *Cephalosporium* has been described. The colony at maturity is pinkish grey. The conidiophores are borne on sharply

differentiated funiculose structures and the conidia are roundish to elliptical with flattened bases. Cultural behavior was noted on several common media. Germination of spores was also studied.

ACKNOWLEDGMENTS

The writer expresses his gratitude to Dr. R. K. Saksena for kindly help and guidance. He is thankful to Dr. Charles Thom for kindly going through the description and the diagrams and to Prof. Fr. H. Santapau for the Latin diagnosis.

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A NEW GENUS IN THE ASPERGILLACEAE¹

FLOYD M. CLUM

In the course of a study of certain aspects of damping-off in a number of garden ornamentals an isolation was made from a seedling of *Phlox drummondii* Hook., grown from a packet of seed marked "Mixed Colors" supplied by Northrup King and Company, that showed the characteristic symptoms of damping-off. As a result of efforts to identify the isolated organism, the conclusion has been reached that it cannot be referred to any known genus but may be tentatively placed in the Aspergillaceae.

It is characterized by an astomous and firm-walled fructification, with globose asci scattered irregularly throughout the cavity. It differs from all other members of this family in the possession of an imperfect stage, a pycnidium. It is from this characteristic of the organism that the generic name *Pycnidiophora* was chosen, derived from *πυκνός* and *φόρος*, meaning "bearer of pycnidia."

The following descriptions of the proposed new genus and species are based on cultures grown on potato dextrose agar and corn meal agar at room temperatures.

Pycnidiophora gen. nov.

Cleistothecia immersa vel *semiimmersa*, per substratum dispersa, globosa, immatura translucentia, matura fusca et opaca, exstiolata; pariete membranaceo, fragili et exappendiculato; hyphae immersae vel aeciae ad substratum appressae; ascis globosis, tenuibus, delicatis, evanescentibus, brevipedicellatis, aparaphysatis, continentibus trigintaduo sporas; sporis conglobatis, simplicibus, oblongo-reniformibus et pallide brunneis; status imperfectus pycnidialis.

Cleistothecia submerged to partially superficial and scattered throughout substrate, globose, translucent when young, dark and opaque when mature, astomous; cleistothecial wall membranous, brittle, and without appendages. Hyphae either submerged or, when aerial, usually closely appressed to substrate surface, the exact nature dependent upon substrate. Asci globose, thin-walled, delicate, evanescent, short-stalked

¹ This paper represents a portion of a dissertation submitted to the School of Graduate Studies, Michigan State College, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

when immature, without paraphyses and with thirty-two spores. Spores conglobate, unicellular, oblong-reniform and light brown in color. Reproductive bodies of imperfect stage pycnidial.

Type species, *Pycnidiophora dispersa*.

Pycnidiophora differs from the genus *Fragosphaeria* Shear by having brown ascospores and a brown, instead of a purple, cleistothecial wall. Although it resembles the genera *Magnusia* Sacc., *Arachnomyces* Massee & Salm., and *Cephalotheca* Fuck., the cleistothecia of this organism do not have appendages. The brown cleistothecium distinguishes it from the genus *Laaseomyces* Ruhl. Conglobate and oblong-reniform spores separate it from the genus *Thielavia* Zopf which produces elliptic spores. None of these genera are known to produce pycnidia.

***Pycnidiophora dispersa* sp. nov.**

Mycelia homothallica, multiramosa; hyphis 1-6 μ in diametro; cleistothecia 60-700 μ in diametro; ascis globosis 10-14.5 μ in diametro; sporis 2.0-2.9 \times 2.8-5.8 μ , immaturis hyalinis et maturis pallide brunneis; pycnidia superficialia, super substratum dispersa, globosa ad irregulariter elongata, glabra, in parte inferiore incolorata, nisi cellulae circa leviter papillatum ostiolum pallide brunneae, 26-78 \times 26-164 μ in diametro; conidiophoris simplicibus, brevissimis; conidia hyalina, simplicia, oblonga, 1.5-3.4 \times 2.6-4.75 μ .

Mycelia homothallic, profusely branched, the hyphae 1-6 μ in diameter; cleistothecia 60-700 μ in diameter; asci globose, 10-14.5 μ in diameter. Ascospores 2.0-2.9 \times 2.8-5.8 μ , hyaline when young, later becoming light brown. Pycnidia scattered on surface of substrate, varying from globose to irregular-elongate in shape, glabrous; the lower portion colorless and the walls of the cells around the slightly papillate ostiole light brown, 26-78 \times 26-164 μ . Conidiophores simple, extremely short. Conidia hyaline, unicellular, oblong, 1.5-3.4 \times 2.6-4.75 μ .

Type specimen: Floyd M. Clum 27, from cultures prepared during study of the organism, deposited in the Beal-Darlington Herbarium of Michigan State College (accession number 133.118); isotype specimens also to be deposited in the University of Michigan and University of Wisconsin herbaria, and cultures are to be sent to the type culture collections in American Type Culture Collection, Washington, D. C., and Centraalbureau Voor Schimmelcultures, Baarn, Netherlands.

The specific epithet refers to the scattered habit of the cleistothecia.

By making single spore isolations of seventeen ascospores and thirty-three conidia, pure strains, identical with the original isolate, were obtained.

When grown on corn meal agar the colony was thin, spreading,

whitish, or translucent, submerged and superficial with little aerial hyphae. After the pycnidia were produced the surface of the colony had a slimy appearance because of conidial production. As the colony aged the blackish cleistothecia developed, scattered or dispersed throughout the medium, giving the colony a speckled appearance.

Upon potato dextrose agar the total characteristics of the colony were very similar to those found in cultures on corn meal agar except that the growth was more dense, the colony color was a dull gray to buff, and more aerial hyphae were produced. The slimy appearance was lacking since the aerial hyphae covered the pycnidia. Cleistothecia were similar in appearance, but larger and more abundant.

Pathogenicity of the organism was established on Aster, Phlox, and Regal Lily. Seedlings of these plants, when grown in Erlenmeyer chambers inoculated with the fungus, often became diseased. Symptoms of the disease were typical of damping-off with a water-soaked appearance of the stem at or just below the soil line. If the seedling was allowed to remain in the chamber then this water-soaked appearance gradually progressed upward in the stem. Infection in the cotyledonary leaves showed the water-soaking and chlorosis.

In every case where these diseased seedlings were plated out on water agar, an organism, similar in every aspect to the parent culture, was re-isolated. Microscopic examination of the diseased host tissue revealed the hyphal strands permeating through the tissues and even some evidence of cell wall penetration.

It has been determined that the pycnidial development is simple meristogenous and that cleistothecial development is much the same except that the latter primarily develop on submerged hyphae while the pycnidia develop on superficial hyphae.

The author wishes to acknowledge the assistance of Dr. Constantine J. Alexopoulos, Michigan State College, who suggested the generic name; of Dr. E. A. Bessey, Michigan State College, for helping with the Latin descriptions; of Dr. Myron P. Backus, University of Wisconsin, who kindly examined the cultures and slides of *P. dispersa*; and of my wife Elizabeth Bell Clum for clerical assistance.

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A NOTE ON CLITOCYBE ADIRONDACKENSIS

HOWARD E. BIGELOW¹

(WITH 3 FIGURES)

During the course of a taxonomic revision of the North American species of *Clitocybe*, some interesting information has been obtained on *C. adirondackensis* (Pk.) Sacc. A microscopic examination of the type collection has revealed some unusual vesiculose elements in the cuticle of the pileus. This discovery prompted the study of numerous collections of *Clitocybe* to ascertain if the structure was present in more than one species.

In order to facilitate a discussion of the problems resulting from this investigation, a complete description of *C. adirondackensis* is now given. It is based on a study of the type and 75 additional collections.

CLITOCYBE ADIRONDACKENSIS (Pk.) Saccardo, Sylloge Fungorum 5: 180. 1887. Figs. 1-3.

Agaricus adirondackensis Peck, N. Y. State Cab. Rept. 23: 77. 1872.

Clitocybe caespitosa Peck, N. Y. State Mus. Rept. 41: 61. 1888.

Clitocybe Kühneri Singer, Ann. Myc. 41: 23. 1943.

Pileus: 1-6 cm broad, plane or convex at first, soon becoming sub-infundibuliform to infundibuliform, margin inrolled at first, remaining decurved or becoming elevated, at times incised, usually not striate but slightly so at times, cuticle separable, surface appearing glabrous when moist, innately fibrillose when faded, at times subviscid, usually with a satiny luster, color near umber when young and moist, gradually paler to "avellaneous" and then changing into the buff series through "isabella color" to "cream buff," "light buff," "cartridge buff," "warm buff," "pinkish buff" or "vinaceous buff," hygrophanous, whitish to pallid when faded, disc often remaining dark.

Flesh: thin, concolorous with the pileus, moist when fresh, usually tapering gradually to the margin of the pileus from the disc; taste unpleasant, odor strong, resembling that of fish, or somewhat spermiatic to rancid-farinaceous.

¹ Paper from the Herbarium, Biological Station, and the Department of Botany, University of Michigan, Ann Arbor, Michigan.

Lamellae: short decurrent at first soon becoming evenly to unevenly long-decurrent, often forming a collar on the apex of the stipe, usually close or crowded, rarely subdistant, forked, sometimes intervenose, straight to somewhat undulate, narrow, thin, brittle, separable from the pileus trama, concolor with the pileus or somewhat paler, edges even.

Stipe: 1-5(-7) cm \times 2-7(-9) mm at the apex, equal or enlarged above, the base usually somewhat enlarged and not radicating, usually terete, solid-stuffed becoming hollow, usually central, surface appearing glabrous when moist then somewhat minutely fibrillose when faded, concolorous with the pileus or paler, bases often fused together, with copious basal tomentum which appears water-soaked when moist and binding the surrounding debris.

Spores: print white (becoming somewhat creamy with age in herbarium); elliptical to pyriform in face view, sublacrymoid in side view, smooth, hyaline, thin-walled, not amyloid, contents granose in KOH, apiculus short and somewhat curved from the side, (4-)4.5-6.5(-8) \times (2.5-)3-4(-4.5) μ .

Basidia: usually four-spored, (12.5-)16.5-24(-32) \times 3-7 μ , occasionally one- or two-spored; sterigmata long and slender (up to 7 μ long), occasionally germinated.

Cystidia: cheilocystidia rare, filamentous, walls slightly thickened, septa and clamp connections rare, usually unbranched, 1.5-3 μ diam., projecting up to 60 μ .

Pileus tissue: cuticle rather thick, mostly composed of narrow cylindrical hyphae, 1.5-6 μ in diam., cells long (\pm 100 μ), with clamp connections, thin-walled, contents often granose; vesiculose elements present in the cuticular region, arising from cuticular or tramal hyphae, near surface, abundant, and more or less evenly distributed, mostly terminal on hyphal tips but occasionally intercalary, globose to elliptical or pyriform or obovate, at times irregularly so, with refractive content which appears localized in a central mass in fresh specimens but which is apparently diffuse in most material revived in KOH and Melzer's solution, walls smooth and thin, usually with a clamp connection on the adjoining cell, 10-30 μ in diam.; trama interwoven with mostly cylindrical hyphae, thin-walled, with clamp connections, cells usually rather long, contents often granose and appearing red-brown in mass in Melzer's.

Gill trama: regular, hyphae mostly cylindrical, with clamp connections, thin-walled, contents often granose and appearing red-brown in Melzer's, 2-10 μ in diam.

Stipe tissue: cortex rather thin, hyphae parallel with the long axis and compactly arranged, cylindrical, thin-walled, with clamps, cells long, 2-4 μ in diam., with very scattered vesiculose elements having the same characters as those in the pileus cuticle, sections of cortex somewhat

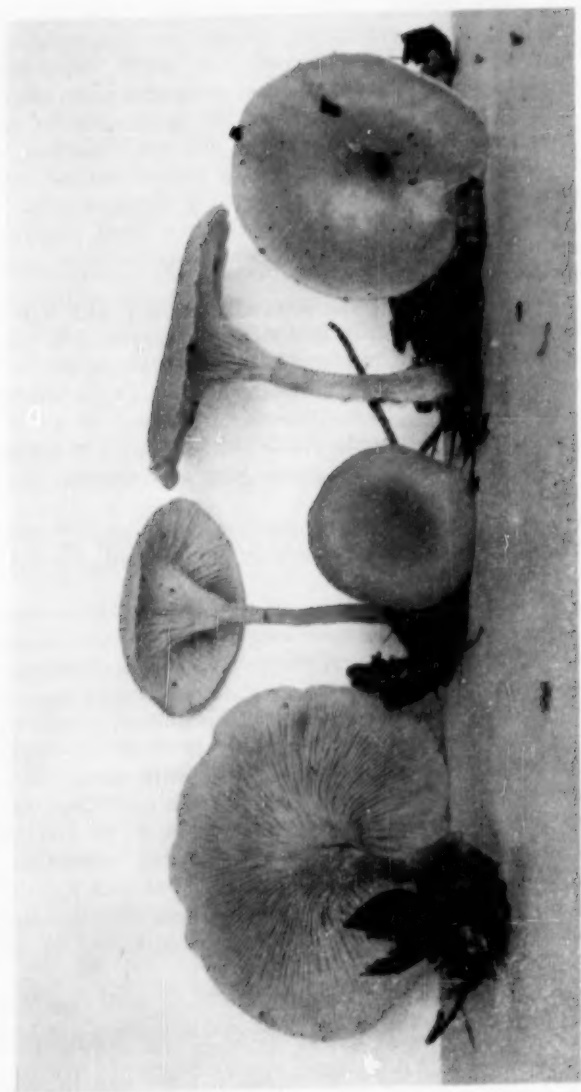
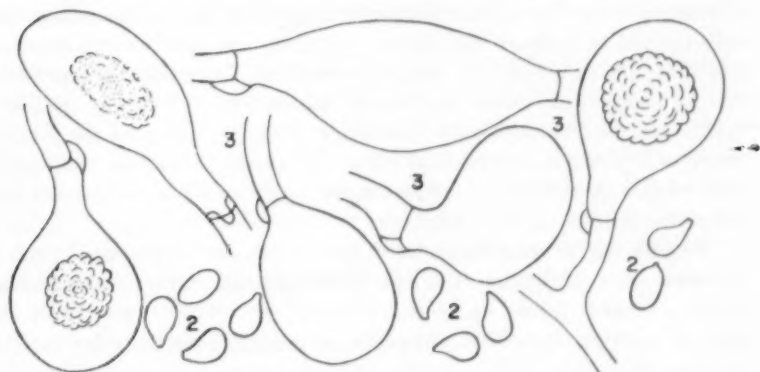


FIG. 1. *Clitocybe adirendackensis* (Pk.) Sacc., $\times 1$. Photo by A. H. Smith.

red-brown in Melzer's; central portion compact except at the center, hyphae cylindrical to somewhat inflated, thin-walled, with clamp connections, cells long, 2–10 μ in diam.

Basal tomentum: interwoven in a mat over the stipe base and surrounding substrate, hyphae loosely interwoven or in small bundles, rather brownish in mass in Melzer's, cylindrical with clamp connections, cells long, thin-walled, 1.5–6.5 μ in diam.

Habit, habitat and distribution: Usually gregarious to caespitose, rarely scattered or solitary. Most frequent under hardwoods, less so under conifers. Mostly on debris and humus, rarely on dung, wood, or in the grass. July to November. Common. Northeastern, eastern, and North Central United States south to Tennessee; Southeastern Canada; Europe; Scandinavia; North Africa.



FIGS. 2, 3. 2. Spores of *C. adirondackensis*, $\times 1000$. 3. Vesiculose elements in the pileus cuticle of *C. adirondackensis*, with and without refractive contents, $\times 1000$.

Material examined: H. E. Bigelow: 390, 624, 629, 649, 735, 1214, 1216, 1223, 1230, 1239, 1336, 1340, 1347, 1348, 1369, 1370, 1371, 1372, 1374, 1385, 1390, 1437, 1504, 1512, 1528, 1529; H. Dykeman: Ann Arbor, Mich., August 13, 1921; J. W. Groves: F9743, DAOM 34585; P. Harding: 257, 273; L. R. Hesler: 14031; H. Imshaug: 3420; M. Jossierand (comm.): October 19, 1934 (as *C. hydrogramma*); C. H. Katuffman: Marquette, Mich., September 1, 1906 (2 collections), Ann Arbor, Mich., September 6, 1907, Ann Arbor, Mich., August 13, 1915; H. Kelly: 725, Magnetawan, Ontario, Canada, September 12, 1921; S. Lundell: Fungi Exsiccati Suecici, Praesertim Upsalienses 1730 (as *C. candicans* forma); E. B. Mains: 31–689, 32–511; G. Malençon: 1223

(as *C. hydrogramma*); W. A. Murrill: 529; C. H. Peck: Type of *A. adirondackensis*, Type of *C. caespitosa*, Karner, N. Y., East Berne, N. Y., Bolton, N. Y.; L. H. Pennington: Ann Arbor, Mich., August 14, 1909; V. Potter: 3598, 3622, 3715, 3937, 3952, 4113, 4237; A. H. Smith: 7205, 7209, 7594, 18590, 31915, 32861, 33059, 33354, 33669, 36035, 38133, 42744, 42748, 42809, 42877, Washtenaw Co., Mich., July 11, 1929, Rock River, Mich., September 8, 1929, Rock River, Mich., September 19, 1929.

DISCUSSION

The vesiculose elements in the cuticle have been noted by European mycologists for such species as *Omphalia hydrogramma* (Fr.) Quélet, *Clitocybe hydrogramma* (Fr.) Kummer, *Clitocybe gallinacea* sensu Kühner, *Clitocybe Kühneri* Singer. In 1942, Malençon (5) summarized much of the information regarding these species and concluded, with the aid of Kühner and Maire, that only one species was involved and that the name of this species should be *Clitocybe hydrogramma* (Fr.). Singer (7) later established the section *Bulluliferae* in *Clitocybe*. He used the name *C. Kühneri* at first, but accepted the French usage of *hydrogramma* in 1949 (8). Lange (4) describes and illustrates *hydrogramma* as an *Omphalia*, while Kühner and Romagnesi (3) place this species in *Clitocybe*.

Besides the unusual character of the cuticle, the European *C. hydrogramma* sensu Malençon *et al.* is considered to have the following diagnostic features: pileus up to 6 cm broad, infundibuliform, deeply depressed, margin somewhat striate or not, hygrophanous, color whitish to buff; flesh thin, with a strong and unpleasant odor resembling that of fish or *Tricholoma sulphureum*; lamellae strongly decurrent, whitish; stipe whitish; spores $5-6 \times 2.5-3 \mu$, not amyloid. Common, on leaves.

When the description and illustrations of *C. hydrogramma* sensu Malençon *et al.* are compared to those of *C. adirondackensis* (Pk.) Sacc. there is agreement on almost all characters. Deviations, in regard to pileus color, size of some of the component elements, variety of habitat, etc., can readily be accounted for. The technique of mass collection, in the case of *C. adirondackensis*, has merely resulted in a more complete description. In this light, *C. hydrogramma* sensu Malençon *et al.* must be regarded as the same fungus as *C. adirondackensis* (Pk.) Sacc.

When *C. adirondackensis* is compared with the Friesian *Agaricus hydrogrammus* there are serious discrepancies. The original description of the latter (1), and the plate in the *Icones* (2), refer to a species

with a long-radically strigose stipe. The stipe of *C. adirondackensis* is never attenuated to an almost rootlike prolongation, but is even or slightly enlarged at the base. The copious mycelium at the base of the stipe is tomentose and never strigose. The margin of the pileus of *A. hydrogrammus* is long-striate, whereas the margin in *C. adirondackensis* is only slightly striate at times, usually not at all. Peck's species has a strong unpleasant odor, while Fries did not mention any odor at all for his *hydrogrammus*. These differences indicate that two different species are involved. In my opinion, the Friesian epithet, *hydrogrammus*, should be retained for the fungus that Fries described.

I have examined the type material of *Clitocybe caespitosa* Peck (6), and find it to be identical microscopically with the type of *C. adirondackensis* Peck. Among my collections of *C. adirondackensis* are several in which the fruiting bodies are caespitose, and these agree in this as well as other macroscopic characters with Peck's original description of *C. caespitosa*.

The faded form of *C. adirondackensis*, which is the form most frequently collected, is often confused with *C. catina* (Fr.) Quél. and *C. phyllophila* (Fr.) Kummer. The descriptions and illustrations of these two species do show some similarities with those of *C. adirondackensis*, but the lack of type specimens for *C. catina* and *C. phyllophila* makes it impossible to determine which of the various concepts that exist at present is the right one. The concept of *C. adirondackensis* is authenticated by type material at Albany.

CLITOCYBE ADIRONDACKENSIS var. **Wernerii** (Mlçn.) comb. nov.

Clitocybe hydrogramma var. *Wernerii* Malençon, Bull. Soc. Myc. Fr. 58: 36. 1942.

The variety *Wernerii* is distinct enough from *C. adirondackensis* to warrant recognition at the varietal level. Dr. Malençon has kindly loaned me authentic material, as well as his original notes, and I am indebted to him for the opportunity of examining these. Variety *Wernerii* differs in having a more virgate pileus surface, somewhat broader and more distant lamellae, and generally more robust aspect. The odor is of *Tricholoma sulphureum* (i.e. coal tar). The spores are less lacrymoid in dorsi-ventral view, and average somewhat larger in size. The dark color of the pileus is within the range of that found for variety *adirondackensis* in this country, so that color cannot be considered diagnostic as Malençon himself originally mentioned. The cesp-

tose manner of growth and the grassy habitat are likewise in this category. *C. adirondackensis* variety *Werneri* has not been found in North America.

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JOHN DEARNESS

W. F. TAMBLYN¹

(WITH PORTRAIT)

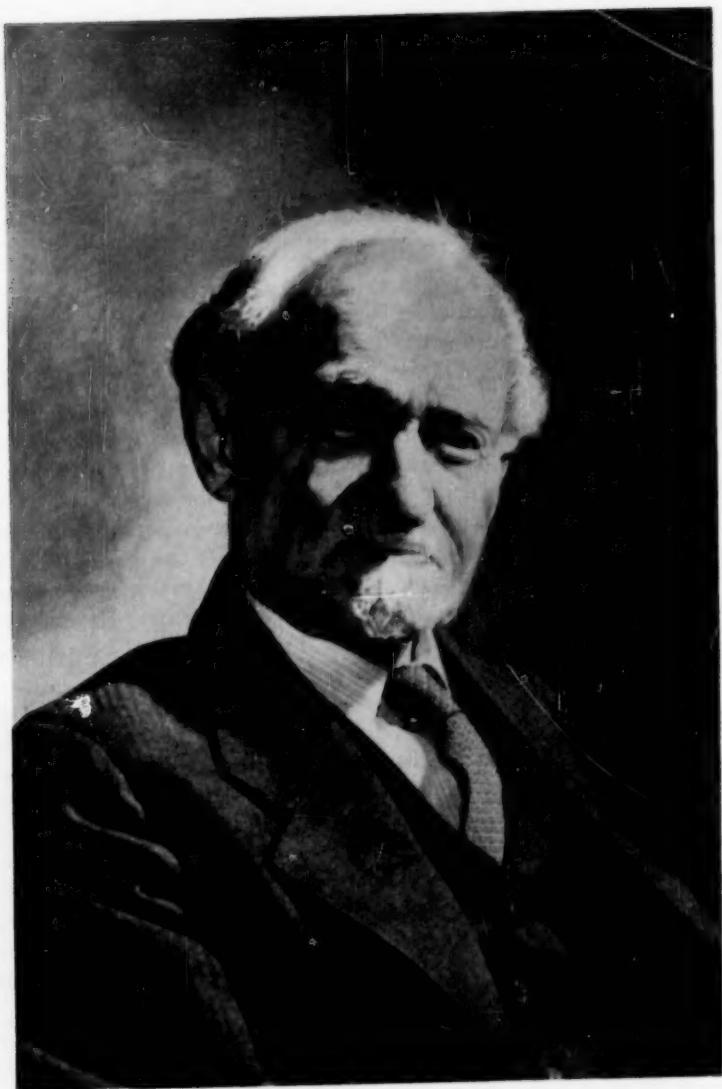
The death of Dr. John Dearness at his home in London, Ontario, on December 6th, 1954, brought to a close a long career. He was an educationist of wide reputation, a botanist, eminent mycologist, and with his varied interests and practical energy an intellectual leader.

Born of Arcadian parents in Hamilton, Ontario, May 13, 1852, he went with them at the age of four to live on a farm about 20 miles north-east of London. He has said that from his sixth year he kept a wild-flower garden of his own. He attended a rural school from 6 to 16 years of age off and on, doing a man's work on the farm at 14 or 15 years. Then, having secured some text-books, he prepared himself for teachers' examinations at London. Later, in 1871, he passed first in a three-months course at Toronto Normal School, winning also a "Special Certificate," rare at that time, "in Natural History, Botany, and Agricultural Chemistry." An instructor, Dr. Kirkland, said some years after, he was "the best student I ever had anywhere."

At the age of 19 John Dearness became Principal of Lucan village school. At 21 he was appointed Principal of Strathroy public school. The High School Entrance class, which he personally taught, refused to take the Entrance examination in the following summer, 1874, as they would not be separated from their beloved teacher. The Strathroy Board of Education and the Ontario Department of Education finally agreed to promote both teacher and class into the High School. Only two or three months did he stay there, for in December, 1874, he was appointed Public School Inspector of East Middlesex. This position he occupied for the next 25 years. From 1888 to 1914 he was also Professor of Biology in the Medical School of Western University.

In the 1880's he engaged himself more and more in botanical studies, exploring the countryside and making collections. He developed intense interest in mycology, microbiology, entomology and phytopathology. He began publishing, along with J. B. Ellis, on Canadian fungi, in the

¹ Son-in-law of Dr. Dearness; former head of the Department of English of the University of Western Ontario.



JOHN DEARNESS
on his 100th birthday.

1890's. He was also doing occasional articles on educational subjects. His activity in entomological study led to his appointment by the Ontario Government in 1899 to the San José Scale Commission.

In 1881 had taken place his marriage with Harriet Emma Wilkinson. She was a great help to him in his botanical work, and a woman of notable graciousness and charm. Of this marriage there are three children, two daughters and a son.

Mr. Dearness was a friendly man and a good co-operator and collaborator. He was a charter member and later in life, Honorary President of the London Baconian Club, the London Canadian Club, the London and Middlesex Historical Society; member and Hon. President of the London Current Topic Club, McIlwraith Ornithological Society, President of the Ontario Educational Association (1896-7), Secretary of the Ontario Branch of the British Simplified Spelling Society, President of the Entomological Society of Ontario (1897-8), President (1912-14) and Hon. President (1952) of the Ontario Historical Society, Hon. Historian of the University of Western Ontario, Vice-President of the Nature Study Association of America, President of the Canadian Division of the American Phytopathological Society (1912-14, 1927), President of the Mycological Society of America (1937), Honorary member of the Canadian Microbiological Society (1953). In 1893 he was placed in charge of Ontario's educational exhibit at the Chicago World Fair.

At the end of 1899 Inspector Dearness was appointed Vice-Principal of the London Normal School. Here he was an immensely popular teacher. At the same time he secured by extramural study the degrees of B.A. (1902) and M.A. (1903) from Western University; and also his writings on both education and mycology increased in number. He was an associate editor of *THE NATURE STUDY REVIEWS* (Ithaca) and of *MYCOLOGIA* (1909-1930). Among his numerous books and articles on nature study the most generally known is "How to Teach the Nature Study Course" (Copp, Clark, Toronto, 1905). His contribution to the Government Report (1923) on the Canadian Arctic Expedition of 1913-18 is important.

He found time to edit a posthumous volume of poems by Robert Elliott, his friend and naturalist-disciple (1905). At the Normal School he made good use of the X-ray machine and the telescope both for his own intellectual curiosity and for the doctors and general public. The University of Toronto had him as examiner in biology at the Ontario Agricultural College. He was in constant demand as a lecturer, and conducted summer schools all the way from Brandon, Manitoba, to

Truro, N. S. One "summer off," so to speak, he botanized on the Magnetawan River with Dr. H. A. Kelly of Baltimore. His long labors with microscope over bushels of specimens sent to him for identification or consultation by mycologists everywhere probably caused some weakening of his eyes in the last two or three years of his life. From 1917 to 1943 the British *Who's Who* had a considerable article on him, and he was listed also in the German *JAHRBUCH DER GELEHRTEN DER WELT*.

From 1902 to 1939 he was auditor of the Ontario Educational Association (O.E.A.). He was a member of the University of Western Ontario Senate and of the Ontario Advisory Council of Education (1909-). In the midst of all this, in 1918 he was advanced to the Principalship of the Normal School, and in 1922, having reached the retiring age, was superannuated by the Ontario Government. Shortly after, the University of Western Ontario (formerly Western University) added to his B.A. and M.A. degrees that of LL.D. He had long before been known commonly as Doctor, and now he had a technical right to it. He had become an oracle and it was not long before they began to refer to him as "Mr. Education" or the G.O.M. In his latest years the annual event of his birthday was elaborately celebrated by the London *Free Press* and Toronto papers, especially the 90th and 100th years.

Naturally he disliked retirement. His health was excellent, and though it had been and still would be sometimes broken by colds and slight illnesses, he never lost any time to speak of from his work. Shortly after he was 70 a brief attack of pneumonia put him to bed for a few days, during which, when he thought of something, he now and then arose, went to his study close by and looked into a book or his microscope. No doctor, nurse or even his wife could stop him.

Many writings on fungi followed the superannuation date, 1922. Among them, most noteworthy, perhaps, were articles in *MYCOLOGIA* (1911-46); contributions to the volumes on fungi of Manitoba and Saskatchewan by himself, Bisby, Buller and others (1929 and 1938); Summary of the Prevalence of Plant Diseases in Canada (Canadian Department of Agriculture Bulletin 71: 62-76, 1926).

He attended some of the mycological "forays," on one of them (1936) accompanied by Mrs. Dearness. When they climbed a mountain with the others they were both complimented on their vigor at their time of life.

In 1931 their family had celebrated their Golden Wedding, having

a picnic at the scenic Oxbow Creek near London. When their 60th Anniversary rolled round, Mrs. Dearness lay in her last illness, to live just a month longer.

In 1926 Mr. Dearness taught a barely five-year old grandson to read and typewrite in three weeks, and made a report on this to the O.E.A. meeting at Toronto. Pictures of himself and grandson appeared in newspapers all the way from Toronto to Boston, in some cases Bobby "stealing the show" from his grandfather. As a teacher, Dr. Dearness seemed to put a spell on a class or an individual. Like Shakespeare's Prospero he was a magician, but gentle, never rough. In his early teaching days he never laid a finger on a pupil, nor did he as inspector advise corporal chastisement. Like Othello he might say, "This only is the magic I have used," love, intent purpose, and preparedness.

Honors came fast upon him in his last 20 years. He received in 1935 the King's Medal, and in the following year the London McIlwraith Society held a complimentary Banquet for him. A well annotated copy of McIlwraith's book on Canadian Birds (1894) was in his library.

In 1936 also he was elected a Fellow of the Royal Society of Canada, and in 1937 he became a member of the A.A.A.S. In his 100th birthday the latter Society sent him an Address and made him a Life Honorary Member. In 1941 the Dearness Research Laboratory in the Montreal Botanical Garden was formally opened and his speech on the occasion was fully reported and praised in the Montreal press.

On his 90th birthday (1942) a reception was tendered him in London, attended by representatives of some dozen institutions and organizations, the City, the University of Western Ontario, the London Normal School, the Public Library, the Ontario Education Department, the Ontario Educational Association, &c., &c. His 100th birthday brought him presents, telegrams, cards and letters from over 500 admirers all over America and beyond. A final demonstration of esteem from his home city was the City Council's naming of "The John Dearness Home for Elder Citizens," a very handsome structure which was dedicated in his honor in June 1953, he himself present on the platform.

In his last two years his hearing and eyesight deteriorated, his general strength declined. This was sad for one who had been so keen in gardening and field work, whose hand was as quick as his mind, who in winter shovelled his own sidewalks cleaner than any others on the block, who at 95 years cut down and sawed up a 6 inch thick walnut tree, who had read so much and with his microscope added so much to scientific knowledge. But he took the end with calm acceptance.

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NOTES AND BRIEF ARTICLES

WOUND-HEALING OF HYPHAE IN A PHYCOMYCETOUS MYCORRHIZAL FUNGUS

Wound-healing in fungus hyphae was first demonstrated by Buller.¹ He found that when small sections of hyphae of *Pyronema confluens* (Pers.) Tul. were killed by pressing with a cold needle, intrahyphal hyphae grew from the septa of the living sections into the cavities of the dead cells. Two intrahyphal hyphae usually grew toward each other simultaneously and met and fused with one another near the middle of the dead hypha. Prior to Buller's studies, many workers had reported observing young slender hyphae running through the cavities of older, thicker dead parts of hyphae, indicating that this type of wound-healing occurs in many species of fungi. Dodge² published a list of fungi in which intrahyphal hyphae had been observed.

While studying the phycomycetous mycorrhizal fungus³ an entirely different type of wound-healing was observed. When growing in water culture or near artificially inoculated plant roots, hyphae frequently grew around hyphal sections that appeared dead, and met and fused with each other. These "bridges" were seldom observed when the fungus was grown on agar. The process appeared similar to that described by Buller except the connecting hyphae were external to the dead sections.

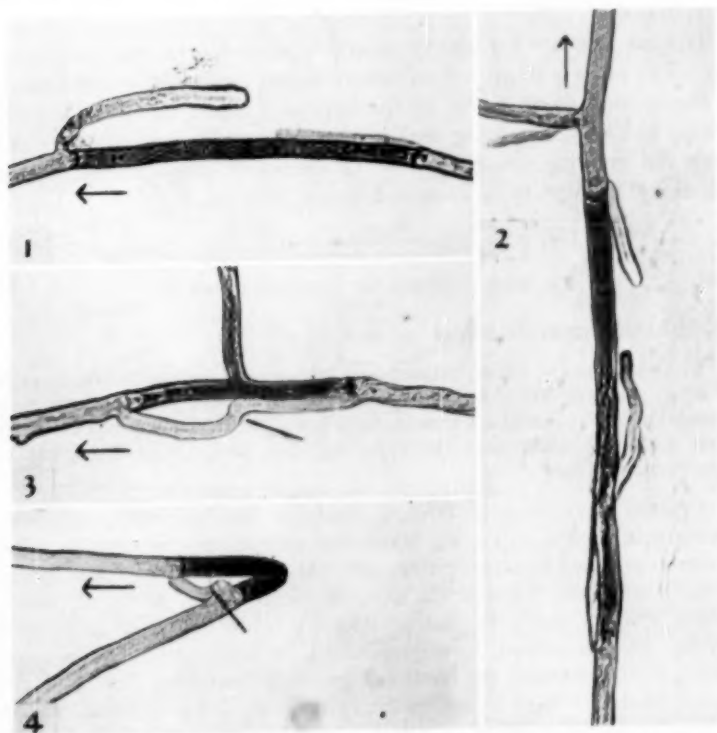
Wound-healing in the phycomycetous mycorrhizal fungus was studied experimentally by artificially wounding hyphal sections. Type B spores obtained from field soil were surface sterilized as previously described³ and plated on hemp seed agar (2 hemp seeds in 10 cc of water agar). The spores germinated after 2 or 3 days and on the 4th or 5th day the hyphae were wounded by drawing a cold needle across them. This resulted in dead sections of hyphae of varying lengths. Shortly after wounding, the color of the injured sections changed from light yellow to brown and within 15 minutes they were separated from the uninjured hyphae by septa. In 4 or more hours hyphae grew from the living

¹ Buller, A. H. Reginald. 1933. Researches on Fungi. Longmans, Green and Co., London. Vol. 5, Part 1: 1-167.

² Dodge, B. O. 1920. The life history of *Ascobolus magnificus*. *Mycologia* 12: 115-134.

³ Gerdemann, J. W. 1955. Relation of a large soil-borne spore to phycomycetous mycorrhizal infections. *Mycologia* 47: 619-632.

sections just behind the cross-walls and followed along the dead sections until their growing points met and fused. Generally, hyphae grew first from the hyphae which were separated from the spores by dead sections. Such hyphae always followed very closely along the dead tissue as they grew back toward the spores. A short time later hyphae grew from the living sections attached to the spores. The hyphae growing away from the spores seemed less attracted to the dead sections and usually grew a short distance away from them (FIGS. 1, 2, 3). As the hyphae



FIGS. 1-4. Growth of hyphae around sections of hyphae killed with a needle. The positions of the attached spores are indicated by arrows. Points at which fusion of growing points occurred are indicated by inked lines. All $\times 270$. 1. Growth of hyphae 7 hours after wounding, showing the relative attraction of the dead section to the hypha growing from the living section connected to the spore (left), and to the hypha growing from the section separated from the spore by dead tissue (right). 2. Growth of hyphae around a dead section 11 hours after wounding. 3. Fusion of hyphae 8 hours after wounding, showing that the growing points curved to meet each other. 4. Fusion of hyphae 5 hours after wounding.

approached each other, their growing points became attracted to each other and they grew together and fused at their tips (Figs. 3, 4). Fusion occurred only between growing points and hyphal tips were never observed to fuse with the lateral walls of hyphae.

Occasionally when hyphae were wounded they died from the point of the wound to the spore. When this occurred, hyphae from the living sections followed the dead hyphae back to the spores for as much as 800 μ . Such hyphae appeared unable to penetrate spore walls; however, several times they fused with tips of new germ tubes produced from the spores.

Hyphae that are completely separated from spores soon stop growing. The process of growth in culture seems to depend on the transfer of stored food from spores to the hyphae. Thus, the wound-healing process aids in maintaining the lines through which food must move to reach the growing points.—J. W. GERDEMANN, Department of Plant Pathology, University of Illinois, Urbana, Illinois.

A NEW SPECIES OF *HELICOBASIDIUM*

Helicobasidium corticioides sp. nov.

Fructificatione late effusa, indeterminata, subcarnosa, sicca aridocarnosa, pallida vel flava; pileo 100–1000 μ crasso; hyphis hyalinis, septatis, ramosis, 3–6 μ diam.; hymenio indistincto; basidiis circinatis, dein 2–3-septatis, 80–160 \times 6–11 μ ; basidiosporis ovatis vel cylindraceis, lateraliter depresso, 14–22.5 \times 6.5–12.5 μ , per mycelium germinantibus.

Fructification broadly effused, margins indeterminate, sub-fleshy, drying arid fleshy, appearing somewhat pelliculose, cremeus to ochroleucous, corticioid in aspect; in section 100–1000 μ thick; hyphae hyaline, septate, branched, without clamp-connections, 3–6 μ in diam., bearing basidia apically and proliferating laterally below the basal cells of the basidia; basidia arched, loosely spiralled, or forming one or two coils, mostly 2- to 3-septate, the basal cell generally becoming devoid of cytoplasm, 80–160 \times 6–11 μ ; epibasidia cylindrical, 2–4 μ in diam., variable in length; spores ovoid to cylindric, adaxially flattened, hyaline, 14–22.5 \times 6.5–12.5 μ , germinating by the production of a germ tube.

COLORADO: Cameron Pass, July 11, 1952 on spruce log, R. W. Davidson, Colo. 752, TYPE; Chambers Lake, east of Cameron Pass, July 11, 1952 on lodgepole pine (?), R. W. Davidson, Colo. 766; Cameron Pass, July 17, 1952 on fir log, R. W. Davidson, Colo. 784; Cameron Pass, July 17, 1952 on alpine fir log, R. W. Davidson, Colo. 788; Cameron Pass, July 17, 1952 on spruce log, R. W. Davidson, Colo. 791; Rocky

Mt. National Park, July 30, 1952 on alpine fir log, R. W. Davidson, Colo. 833; Turkey Creek, near Redcliff, July 21, 1953 on *Abies lasiocarpa*, P. L. Lentz, Colo. 1248. WYOMING: Mullen Creek, Medicine Bow Mts., Carbon Co., August 13, 1939 on conifer pole, W. G. Solheim (Rocky Mt. Herbarium 1804).

This species is distinguished from other species of *Helicobasidium* by the corticioid aspect of the fructification, the basidia, which are usually

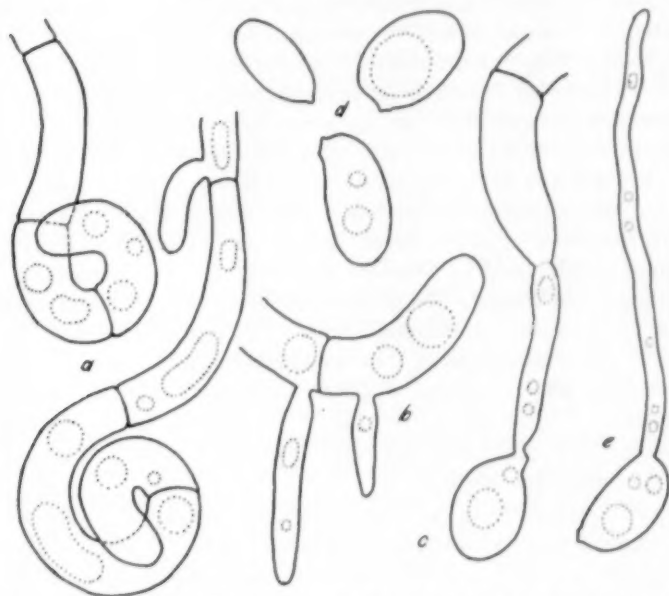


FIG. 1. a. Two developing basidia. b. Basidial cells with epibasidia. c. Apical cell of basidium, epibasidium, and attached spore. d. Spores. e. Germinating spore. All figures drawn with the aid of a camera lucida and reduced to approximately $\times 1000$.

coiled or loosely spiralled rather than crozier-shaped, and by the size of the basidia and spores.

The specimen collected in Wyoming was examined by H. S. Jackson and he assigned it a manuscript name. However, his combination was never published and the specimen upon which it was based appears to be rather weather-beaten. According to R. W. Davidson, the species is very common in the spruce-fir forests of Colorado.—R. J. BANDONI, State University of Iowa, Iowa City, Iowa.

MONOCHAETIA AND PESTALOTIA^{1, 2}

For many years the writer has been engaged in monographing the genera *Monochaetia* and *Pestalotia*. The studies are near completion and publication is contemplated.

Steyaert, in 1949 (Bull. Jard. Bot. Brux. **19**: 285-354), has arranged the species of *Monochaetia* and *Pestalotia* in three genera, limiting the genus *Pestalotia* to its type *P. pezizoides* De Not., a species with 5-septate conidia and an apothecioid acervulus. Two new genera are erected, *Truncatella* and *Pestalotiopsis* for 3- and 4-septate conidia, respectively, both characterized by simple acervuli without stromatic tissue. The genus *Monochaetia* is eliminated and its species placed in a subsection *Monosetulatae* set up under each of the two new genera.

Servazzi (Nuovo Giorn. Bot. Ital. **60**: 943-947, 1953) disagrees with Steyaert and has given substantial reasons. I, too, cannot agree and add my objections to Steyaert's treatment of this group of fungi. In my treatment of *Monochaetia* and *Pestalotia*, all the new generic designations proposed by Steyaert are relegated to synonymy.

Steyaert has removed the genus *Pestalotia* from the Melanconiaceae to the Discellaceae (Sphaeropsidales). His two new genera are retained in the Melanconiaceae. In my monographic treatment, 4 species of *Pestalotia* and 12 species of *Monochaetia* with 6-celled conidia are recognized. *P. pezizoides*, the type of the genus, has an apothecioid acervulus. We might then ask what disposition is to be made of the other 15 sexloculate species.

Marked variations in the fruiting structure in regard to the amount of stromatic tissue characterize *Monochaetia* and *Pestalotia*. However, the conidia are uniform, with variation essentially in the number of cells. Pycnidial structures are also recognized. There is no accurately defined position for these genera on the basis of fruiting structure in a broad sense, nor is it acceptable to group the species with the same conidial type into distinct genera on the basis of the number of conidial septa. These characters might be retained for defining species. The great majority of the species have simple acervuloid fruiting structures and should be retained in the Melanconiaceae. The literature records numerous proposals to change the position of these genera, but there is no agreement.

Steyaert's genus *Truncatella*, which includes the species with 4-celled

¹ Contribution No. 1007, Mass. Agricultural Experiment Station.

² The writer is indebted to John A. Stevenson, Principal Mycologist in Charge, The National Fungus Collections, U.S.D.A., for proof-reading the manuscript.

conidia or the Quadriloculatae of Klebahn, is subdivided into Mono-setulatae, Bisetulatae, Trisetulatae and Multisetulatae. The same subdivisions are set up for the genus *Pestalotiopsis*, which includes the 5-celled or the Quinqueloculatae of Klebahn. The genus *Monochaetia* is eliminated, and its 4- and 5-celled species distributed among these two genera in the Melanconiaceae. No disposition is made of the twelve 6-celled species of *Monochaetia* except that presumably they would appear as a subsection in the genus *Pestalotia*, which Steyaert has placed in the Discellaceae (Sphaeropsidales).

Species with more than one setulum cannot be grouped or satisfactorily defined on the basis of number since this character is flexible and variable within the same species. The writer firmly believes that *Monochaetia* is a good genus. The single appendage clearly sets it apart from the genus *Pestalotia*. It should be accepted as a good genus in preference to its original status as a subgenus of *Pestalotia*.

Steyaert's treatment of these genera is chaotic and adds too much confusion to a system of classification in dire need of simplification and consistency. His studies place undue emphasis on the host plant as a specific distinguishing character, which in the experience of the writer is undesirable. On this unacceptable basis, new species are constantly added to the literature to create more and more confusion and duplication. The species are ubiquitous and mostly saprophytic, rarely pathogenic. A system of classification independent of hosts is to be preferred.

In my treatment of the genera *Monochaetia* and *Pestalotia*, the hosts are not recognized in the concept of species. Three generic subdivisions are recognized, i.e. 4-, 5- and 6-celled conidial groups. The species of *Pestalotia* with 5-celled conidia are subdivided further into three groups on the basis of color differences. Other more specific differences relate to measurements, setulae and conidial form. The aim is a simple, practical arrangement that will be most useful to plant pathologists, and others concerned with the group.—EMIL F. GUBA, Waltham Field Station, Department of Botany, University of Massachusetts, Waltham, Massachusetts.

TORREY BULLETIN INDEX ¹

The Torrey Botanical Club has just published a thousand-page index of authors, subjects, and names of organisms included in the Bulletin during its first seventy-nine years of publication. Since the Bulletin is

¹ Rickett, H. W., Index to the Bulletin of the Torrey Botanical Club volumes 1-75 (1870-1948). viii + 997 pp. Torrey Botanical Club. 1955. \$15.00.

by far the oldest of American botanical journals, and has always been open to articles on all phases of botany, the Index provides for botanists of all sorts a convenient and indispensable key to a very considerable literature. Mycologists will find important papers by Arthur, Atkinson, Banker, Ellis, Gerard, Peck, Underwood, and numerous other early students of fungi, as well as more recent studies, listed and analyzed. —D. P. R.

BIOLOGIA

A new journal, under the above title, is being established by the Biological Society of Pakistan, Lahore. It will appear twice a year and the yearly subscription is fixed at Rs. 15. The first number contains a report on the Pezizales of West Pakistan (24 pp.) by Dr. Sultan Ahmad, the Editor-in-Chief, and eight other papers, mostly taxonomic, in fields other than mycology.

M. S. A. GRADUATE FELLOWSHIP

The Mycological Society of America announces that it will receive applications for the newly established Graduate Fellowship in Mycology. This fellowship will be awarded for 1956-1957 and carries a stipend of \$750. Eligible candidates must be pre-doctoral students in residence at the institution where they are registered for the Ph.D. degree.

Forms for application may be obtained after January 1st from the Secretary-Treasurer of the Society, Dr. C. J. Alexopoulos, Department of Botany and Plant Pathology, Michigan State University, East Lansing, Michigan. Applications are due by February 15, 1956.

Committee on Research Grants

JOHN EHRLICH

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CORRECTION

The author of the paper "Two new species of *Chaetomium* and one new *Humicola* species" in the September-October issue (47: 748-757) is Aasa Omvik, not Aase Omvik, as printed.

REVIEWS

LABORATORY IDENTIFICATION OF PATHOGENIC FUNGI SIMPLIFIED, by Elizabeth L. Hazen and Frank Curtis Reed. xii plus 108 pp., 22 figs. Charles C. Thomas, Springfield, Illinois. Price, \$5.50.

The pathogenic fungi of the title refers to a limited number of human pathogenic fungi common in North America, 10 species in 3 genera under the general heading of superficial mycoses, and 14 species in 11 genera grouped as deep-seated mycoses. The unit of treatment is the specific disease, with the causal organism listed or, in the case of chromoblastomycosis, four causal organisms. Several species are mentioned as possible causal agents of maduromycosis, but only one is discussed. A few of the more commonly encountered synonyms are listed. Each disease has four pages devoted to it: a condensed summary of macroscopic and microscopic characters, a general statement, a figure and a facing explanatory page. Each figure includes from 1 to 7 separate half-tones from photographs showing cultural characters and microscopic details. A list of commonly used media and a fairly complete selected bibliographical section complete the volume.

There is no index, since the introductory summary serves the purpose, and keys would be superfluous. The intention is to enable medical practitioners to recognize common human pathogens in culture. In this aim the book should be of definite service, provided it is always recognized that it is incomplete. It should also be helpful in general mycology classes, to be used in connection with the Conant manual.—G. W. M.

ERKENNE UND BEKÄMPFE DEN HAUSSCHWAMM UND SEINE BEGLEITER, by Kurt Lohwag. 61 pp., 36 figs., 3 col. pl. with 9 figs. Verlag Georg Fromme & Co., Wien V. Price, \$1.90.

The author's interest in the fungi that cause decay of wood-work in buildings is well known. As a result of the destruction in Vienna during the second World War, the activity of these was greatly increased. The present booklet is directed, therefore, primarily to practical workers interested in controlling and preventing their activities.

About a quarter of the book is devoted to *Merulius lacrymans*, which is believed to be responsible for 80-90% of the total damage of this

sort, but over 50 other species are mentioned and there is a brief discussion of mold damage and of certain chemical effects which simulate fungus injury.

The 36 black and white figures, all from photographs, are mostly excellent; a few are unsatisfactory. The color plates are extraordinarily good.

The book should be of interest to mycologists and applied botanists and could advantageously be used as reference in classes.—G. W. M.

THE STORY OF MOSSES, FERNS AND MUSHROOMS, by Dorothy Sterling. Photographs by Myron Ehrenberg. 159 pp.; about 125 illustrations. Doubleday, New York, 1955. Price, \$2.75.

About a third of this book is devoted to the commoner fungi, including lichens, and somewhat more than a third of the illustrations. The text is clear and simple; the photographs superb. For young people, ages 10 to 15. Recommended as a gift for children interested in nature study.

THE INDEX

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